Dissolved Oxygen in the Chesapeake Bay

Processes and Effects

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Proceedings of a Seminar
on Hypoxic and Related Processes
in Chesapeake Bay

Edited by
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INTRODUCTION

In recent years, seasonal oxygen depletion in Chesapeake Bay has been identified as a major indicator of reduced environmental quality and as a potential stress on the Bay's living resources. Consequently, one of the goals of the on-going federal/state Chesapeake Bay restoration program is the reduction of the extent and duration of these hypoxic events.

However, such management strategies need a sound scientific basis for their development. The processes which lead to the establishment and maintenance of low dissolved oxygen, the relative importance of natural (e.g., climatic) versus anthropogenic forces, and the nature and extent of impacts on living organisms have not been well-understood. In order to fill in these information gaps, the National Oceanic and Atmospheric Administration (NOAA), through the Maryland and Virginia Sea Grant Programs, has been funding a major effort to study the processes and impacts associated with hypoxia and anoxia. This study program, initiated in September 1985, has already begun to shed light on many of these problems.

To begin the process of synthesizing the knowledge gained, Maryland and Virginia Sea Grant jointly sponsored a Seminar on Hypoxia and Related Processes in Chesapeake Bay, which was held January 21 and 22, 1987, in College Park, Maryland. The meeting focused on selected research related to low dissolved oxygen, estuarine processes, and the biological impacts of hypoxia. The primary objectives of the meeting were:

1. To provide for the exchange of ideas, research findings, data, and other information among investigators participating in the Sea Grant Low Dissolved Oxygen Program and related research projects, NOAA's Stock Assessment Program, and the federal/state Chesapeake Bay Monitoring Program.

2. To discuss these findings, their interpretation, and research implications among seminar participants.

3. To encourage future integration and exchange among participating programs and investigators.

The seminar was more than a presentation of individual project results; the intent was for investigators to discuss their research programs, their findings to date, and the relationship of their research to other work. The seminar was organized to facilitate this information exchange, and to stimulate discussion among participants. The latter include principal investigators of pertinent Sea Grant projects, researchers working on related projects with state or other agency support, NOAA stock assessment P.I.s, representatives from the federal/state Chesapeake Bay monitoring program, and other invited attendees. The energetic and information-rich discussions which resulted were an important part of the meeting and are summarized in this document.

This seminar represents the first step in evaluation and dissemination of information gained in the important research program. A more in-depth presentation and synthesis of research results will occur at the end of the current research program.

Recent Trends in Hypoxia

HYPOXIA IN VIRGINIA'S ESTUARIES:
AN ASSESSMENT OF HISTORICAL DATA

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As an initial step in elucidating the dynamics of hypoxia in Virginia's saline waters, a grant was awarded to VIMS to collect and organize historical dissolved oxygen data from the Chesapeake Bay and its subestuaries. The specific objectives of the one year study were:

1. To create a computer-based, data management system for existing dissolved oxygen data in Virginia's saline waters.

2. To document, through the analysis of the historical data, the temporal and spatial characteristics of hypoxia in Virginia's saline waters.

3. To analyze the data set with a view toward defining which environmental processes (natural and anthropogenic) are critical in regulating the hypoxia process.

4. To use the results of this study to guide future research on hypoxia in Virginia.

The compilation and organization of the data have been completed and the analysis of the data is currently underway. The results provided in this report should be considered preliminary and are subject to revision.

Description of the Computer-Based Data Management System

The database for this project was created and managed using the Scientific Information Retrieval (SIR) computer software. SIR is an integrated Data Base Management System (DBMS) with a Fortran-like programming language and can interface with statistical packages such as SPSS and BMDP. The database is hierarchial in structure, i.e., one record owns many other records in a top-down approach (Figure 1). The first record type is referred to as the header record and contains various station information, i.e., river ID, date, cardcode, time, cruise, river, latitude and longitude degrees, minutes and tenths, total depth, Secchi disc visibility, wind direction and speed, and air temperature.

Depth records are organized into the following record types:

Record Type 2 - Temperature
Record Type 3 - Salinity
Record Type 4 - Bacteria
Record Type 5 - Nutrients
Record Type 6 - Organics
Record Type 7 - Algae and Chlorophyll
Record Type 8 - Dissolved Oxygen and pH
Record Type 9 - Suspended Solids and Turbidity
Record Type 10 - Conductivity
Record Type 11 - Inorganics
Record Type 12 - Sample Time
Record Type 13 - Current Direction and Speed
Record Type 21 - Table Look-up

Each depth record observation contains the following information: river ID, date, year, time, cardcode, depth, method code, value and sequence number. Every style of gear and method of analysis is assigned an alpha-numeric code and may be found in record type 21. The rivers and the Bay were divided into 5 nautical mile segments to facilitate spatial analysis of data.

The existing historical hydrographic data base at VIMS, named Hydro, was stored on magnetic tapes and managed by a Prime-supported/DBMS called Power. Because the database was so large it was divided into two-year intervals, except for the years 1942-1962 and 1981-1983, and programs were written to extract and modify the data in the Power format so that they could be loaded into a SIR schema. The schema defined record size, variable names, formats, value ranges, missing values, labels, sort IDs and the relationship between the header record and depth records. Several other sources including Old Dominion University, Hampton Roads Sanitation District and VIMS provided additional dissolved oxygen data.

The data were checked and corrected for duplicated observations; the latitude and longitude were checked against the Hydro segments file and assigned an appropriate segment name (river ID). All the information was sorted and split into the various records and each record type was added one at a time to the database. The database was then unloaded in a sequential format and written to magnetic tape.

Various retrieval programs were written to extract the necessary header information, temperature, salinity and dissolved oxygen (DO) data, making use of the sort ID variables defined in the schema. The data were sorted by river ID, date, time, carcode (an integer assigned to each station) and sequence number. A criterion was established to declare dissolved oxygen values of 4.0 mg/l or less to be low DO values. Salinity, temperature, DO, river ID, depth and date were written to SPSS systems file for later analysis.

Preliminary Results

Oxygen levels less than 4 mg/l occur throughout the Bay proper and its subestuaries almost exclusively at water temperatures above ca. 20C. At this latitude water temperatures above 20C correspond roughly to a time span from May through September. Despite the apparent threshold effect of temperature on low dissolved oxygen, oxygen concentrations appear not to be inversely correlated with temperatures above 20C.

In both the York and Rappahannock, oxygen levels less than 4 mg/l occur primarily in the lower 20 km and 40 km of the rivers, respectively. These sections of both rivers are characterized by water depths of up to 20 m in the main channel, which is considerably deeper than the 5-10 m depth upriver. The close association of low dissolved oxygen with these deep holes at the river mouths is further substantiated by an inverse relationship between dissolved oxygen and water depth in the lower sections of the rivers.

The James River differs substantially from the York and Rappahannock in that oxygen levels less than 4 mg/l are rarely observed in the lower river despite the presence of a deep hole (ca. 20 m) at the mouth. In the James River, low oxygen values are observed predominantly in the upper river, roughly between Hopewell and Richmond. During the 23 year interval covered by the data set, the relative frequency of low dissolved oxygen observations in the upper James River has decreased.

During the ten-year span 1971-1980, the data indicate a gradation of hypoxic stress in the series Rappahannock > York > James. During this period, oxygen concentrations below 4 mg/l in the Rappahannock River were approximately equally distributed above and below 2 mg/l. In the York River, low dissolved oxygen concentrations were predominately between 2 and 4 mg/l. In the James river oxygen concentrations below 4 mg/l were predominately within the range of 3-4 mg/l. This gradient of hypoxic stress is more clearly apparent if the data set is restricted to the lower section of each of the three rivers, since oxygen values less than 4 mg/l were rarely observed in the lower James River.

The relative frequency of oxygen values between 0 and 2 mg/l in the Rappahannock River has increased consistently during the 23 years that data are available. Similar trends were not apparent in the York or James rivers.

The apparent lack of hypoxia in the lower James River, compared to the lower York and Rappahannock rivers, is perhaps surprising given their gross morphometric similarities, i.e., all three rivers have deep holes at the

mouth, and the fact that the James River receives higher loads of BOD and COD from anthropogenic sources than either of the other two rivers. Kuo and Neilson (unpublished manuscipt) suggest that the environmental influence most consistent with the observed gradient of hypoxia in these three systems is the relative magnitude of the longitudinal salinity gradient in the rivers. They point out that the longitudinal salinity gradient, and hence the magnitude of the gravitational circulation, is strongest in the James River and weakest in the Rappahannock River. Consequently, oxygen depletion of upriver-flowing bottom water, primarily via benthic oxygen demand, is least in the James River (short residence time) and greatest in the Rappahannock River (long residence time), giving rise to the relative levels of hypoxia observed in these rivers. Another potentially important factor may be the oxygen concentration of the bottom water entering at the mouth of each river (E.P. Ruzecki, personal communication). Because of its greater distance from the mouth of the Chesapeake Bay, deep water entering the Rappahannock River may be expected to have a lower oxygen concentration, owing to its longer transit time from the mouth of the Bay, than deep water entering the mouth of the James River. These proposed differences in oxygen content of the bottom source water to each river could be expected to contribute to relative levels of hypoxia like those observed.

Both of these explanations for the observed gradient of hypoxia among the James, York and Rappahannock rivers emphasize the important influence of physical rather than anthropogenic processes in regulating oxygen dynamics in these river systems. At present, with phosphate bans, eutrophication, and low dissolved oxygen levels as primary indicators of water quality, it is important to remember that natural physical/hydrographical processes as well as anthropogenic influences may be important when attempting to elucidate the dynamics of a hypoxia process. It is also important to remember that different processes may act to varying degrees in different parts of the Bay; no single model will apply to all regions. Many important parts of the puzzle remain to be quantified (e.g., rates of benthic oxygen demand and sources and rates of carbon supply to the sedi-

ments). The analysis of historical data can help to determine which processes regulating oxygen concentations are important in a given region of the Bay, and which processes need to be (more carefully) quantified to adequately elucidate the cause (and possible amelioration) of hypoxia.
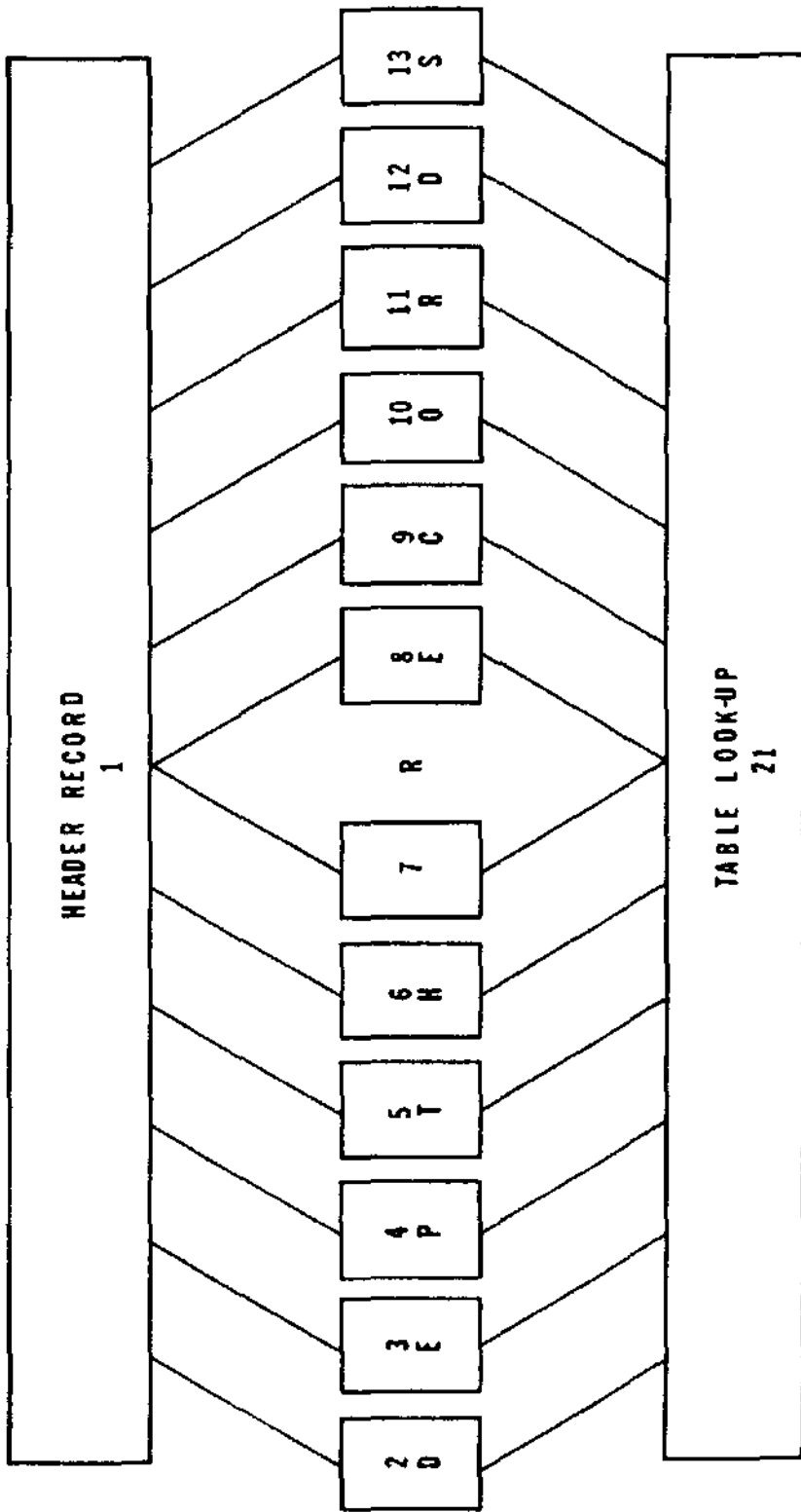
Figure 1. Schematic diagram of database.

CHESAPEAKE BAY MAINSTEM AND TRIBUTARY MONITORING PROGRAM

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The Chesapeake Bay Monitoring Program, initiated in June 1984, is a coordinated network that samples for a variety of water quality, sediment quality and biological resource parameters. The station network covers the entire Chesapeake Bay, from the Conowingo Dam above the Susquehanna Flats down to the Virginia Capes (Figure 1). The goals of the program are to characterize present conditions, detect long-term trends in water quality for documenting the response of the system to remedial actions, and assist in establishing the relationships between water quality and living resources.

Maryland and Virginia Mainstem

Nineteen water quality parameters are currently measured at 28 mainstem stations in Virginia and 22 mainstem stations in Maryland. Eight additional parameters are calculated using these measured values (Table 1). Sampling frequency is twice monthly from March through October and once monthly from November through February -- a total of 20 cruises per year. Cruises are coordinated between Maryland and Virginia with sampling efforts merging at an overlap station off the mouth of the Potomac River. The entire 50 station network is normally covered in three days.

Temperature, salinity, dissolved oxygen and pH are profiled at all mainstem stations. Readings for these parameters are taken at a maximum of 2 m intervals through the water column. Additional measurements at 1 m intervals are taken around the pycnocline, if present.

Grab or pumped water column samples are collected for analysis just below the surface and 1 m above the bottom. In addition, at all 22 Maryland mainstem stations and an axial set of 9 Virginia mainstem stations where stratification normally occurs, two additional samples are taken above and below the pycnocline.

The mainstem stations were situated to represent each of the Chesapeake Bay segments identified during the research phase of the Chesapeake Bay Program. Additional factors guiding station selection included critical areas such as important fisheries habitats, areas experiencing severe anthropogenic impacts, areas experiencing prolonged periods of hypoxic and anoxic conditions, and locations of historical water quality stations.

Table 1. Water quality parameters measured or calculated* at the Chesapeake Bay mainstem monitoring program stations

Temperature	Ammonia
Dissolved oxygen	Total organic carbon
Salinity	Particulate organic carbon*
pH	Dissolved organic carbon
Secchi depth	Total phosphorus
Total Kjeldahl N	Particulate P*
Dissolved Kjeldahl N	Total Dissolved P*
Total nitrogen*	Dissolved organic P*
Particulate N*	Orthophosphorus
Total dissolved N*	Total suspended solids
Dissolved organic N*	Silicon
Dissolved inorganic N*	Chlorophyll a
Nitrite	Pheophytin
Nitrite+nitrate	

Maryland Tributary Monitoring

Maryland has a total of 55 tributary stations, 36 of which are sampled at the same frequency as the mainstem stations. The remaining 19 stations are sampled monthly. The stations that are sampled 20 times per year include all

the Patuxent River and Eastern Shore estuary stations, the Choptank and Chester rivers and selected Potomac River stations. The U.S. Geological Survey collects storm event and monthly baseflow samples at 3 fall-line stations on the Patuxent, Susquehanna and Choptank rivers. The Occoquan Watershed Monitoring Laboratory is responsible for fall-line monitoring at the Potomac River Station. The Maryland tributary stations were located to characterize the salinity and circulation regimes found in the tributaries and to determine environmental characteristics of the smaller rivers flowing into the major tributaries or the Bay.

The same parameters are measured at the Maryland tributary stations as at the mainstem stations with the addition of:

Soluble Aluminum (Fall-line stations)
Biochemical Oxygen Demand (Potomac River fall-line station)
Chemical Oxygen Demand (Potomac River fall-line station)
Total Coliform (Potomac River fall-line station)
Fecal Coliform (Potomac River fall-line station)

Virginia Tributary Monitoring

The Virginia Water Control Board samples the three major Virginia tributaries, the Rappahannock, the York and the James rivers, at 28 stations at the same frequency as the mainstem program. Monthly baseflow samples are also selected at the 4 fall-line stations on the Rappahannock, Mattaponi, Pamunkey and James rivers. The Virginia tributary stations were situated to characterize the salinity and circulation regimes found in the tributaries (tidal fresh, riverine-estuarine transition, lower estuarine) and to determine environmental conditions in the smaller rivers (Appomattox, Chickahominy, Elizabeth, Corrotoman) flowing into these major tributaries.

The same parameters are measured at the Virginia tributary stations as the mainstem stations except as noted below:

Specific Conductance and Salinity (every two meters)
Total Kjeldahl Nitrogen (unfiltered only)
Total Organic Carbon (DOC not measured)
Total Suspended Solids (selected stations only)
Fecal Coliforms (upper James River)

District of Columbia Tributary Monitoring

The District of Columbia monitors 27 stations on the Potomac River, 28 stations on the Anacostia River and 22 stations on several small tributaries. The sampling frequency is the same as for the mainstem program. The District's program is part of the Coordinated Anacostia River Monitoring and the Potomac Regional Monitoring Programs.

Maryland Biological Monitoring

Maryland collects benthic samples ten times each year at 70 stations in the mainstem Bay and tributaries. The benthic stations were situated to coincide with the long term Maryland Power Plant Siting Program benthic monitoring stations and enhance the temporal and spatial coverage of the existing program.

Phytoplankton is sampled twice monthly at 16 stations in the mainstem and tributaries. Zooplankton collections are made monthly throughout the year at the same 16 stations.

Virginia Biological Monitoring

Virginia collects quarterly benthic samples at a subset of 5 mainstem stations and 11 tributary stations. The 16 benthic stations were located in the major salinity-sedimentary regions of the tidal waters within the major Virginia tributaries and mainstem.

Phytoplankton samples are collected 20 times per year at 7 mainstem stations and monthly at 6 tributary stations. Depth integrated zooplankton samples are collected once a month at all 13 of these plankton stations.

District of Columbia Biological Monitoring

In the Potomac and Anacostia rivers and smaller ajoining tributaries, the District of Columbia collects zooplankton and phytoplankton samples at a subset of stations on a monthly basis.

Maryland Sediment Monitoring

Maryland collected sediment samples in 1984 and 1985 at the 22 mainstem stations and in 1985 at selected tributary stations. Further sampling is being delayed for several years due to low temporal variation found under the current sampling frequency.

Virginia Sediment Monitoring

Virginia collected sediment samples once per year at 8 mainstem stations since 1984 and in 1985 at 27 tributary stations. Further sampling is being delayed for several years because of low temporal variation with current sampling frequency.

Long-Term Monitoring Program

There are many other monitoring programs not described within this broad overview of the Chesapeake Bay Monitoring Program. We selected the programs described here because of their significance in monitoring the occurrence of hypoxia and anoxia in the Bay's mainstem and tributaries.

The fixed station network outlined in Figure 1 is only a part of an extensive set of other monitoring and research activities occuring on different spatial or temporal scales. The core programs described here are the framework of the more extensive Bay-wide monitoring program. Related short term scientific research and monitoring activities can be linked to each other through the longer, constant record of water quality and biological resource information being developed by the coordinated Chesapeake Bay Monitoring Program.

There is a growing awareness of the value of long-term ecological monitoring programs, but is there enough support to sustain and maintain this network of stations to answer the questions managers and researchers are asking? The basis of that support must begin within the research community itself. A key question that participants in the Monitoring Program must address in coming years in the definition of "long term" in the context of managing the Chesapeake Bay. Although we need to commit ourselves to a set of stations and an approach to monitoring which will continue with minimal alteration, there is a need for minor refinements of the current monitoring program. We must sustain the coordinated data collection for many years to come with the flexibility to answer other data needs as they arise.

As we begin to understand the temporal characteristics of DO and the mechanisms important in establishing low DO, the water quality and biological resource data collected by the monitoring program can further clarify these initial findings. However, with the current biweekly sampling regime during the critical months, we can't measure many of the short-term events often associated with seiching of the pycnocline. The monitoring program, as it is currently structured, was not set up to examine events occuring on a temporal scale of less than a month. Collectively, we are beginning to examine the use of long-term instrument deployment on moored platforms to improve the temporal and lateral characterization of the mainstem. The use of satellite imagery to increase the program's detection of short term events and to enhance trend analysis is also being actively explored.

The Monitoring Program becomes weakest when we leave the plankton and benthic links in the food chain and proceed to what is often most important to us as users: finfish and shellfish. Special habitat monitoring programs have been set up to provide that linkage. How we can better monitor habitats and biota to detect the biological effects of hypoxia is a questions we hope the joint NOAA/Sea Grant program will begin to answer.
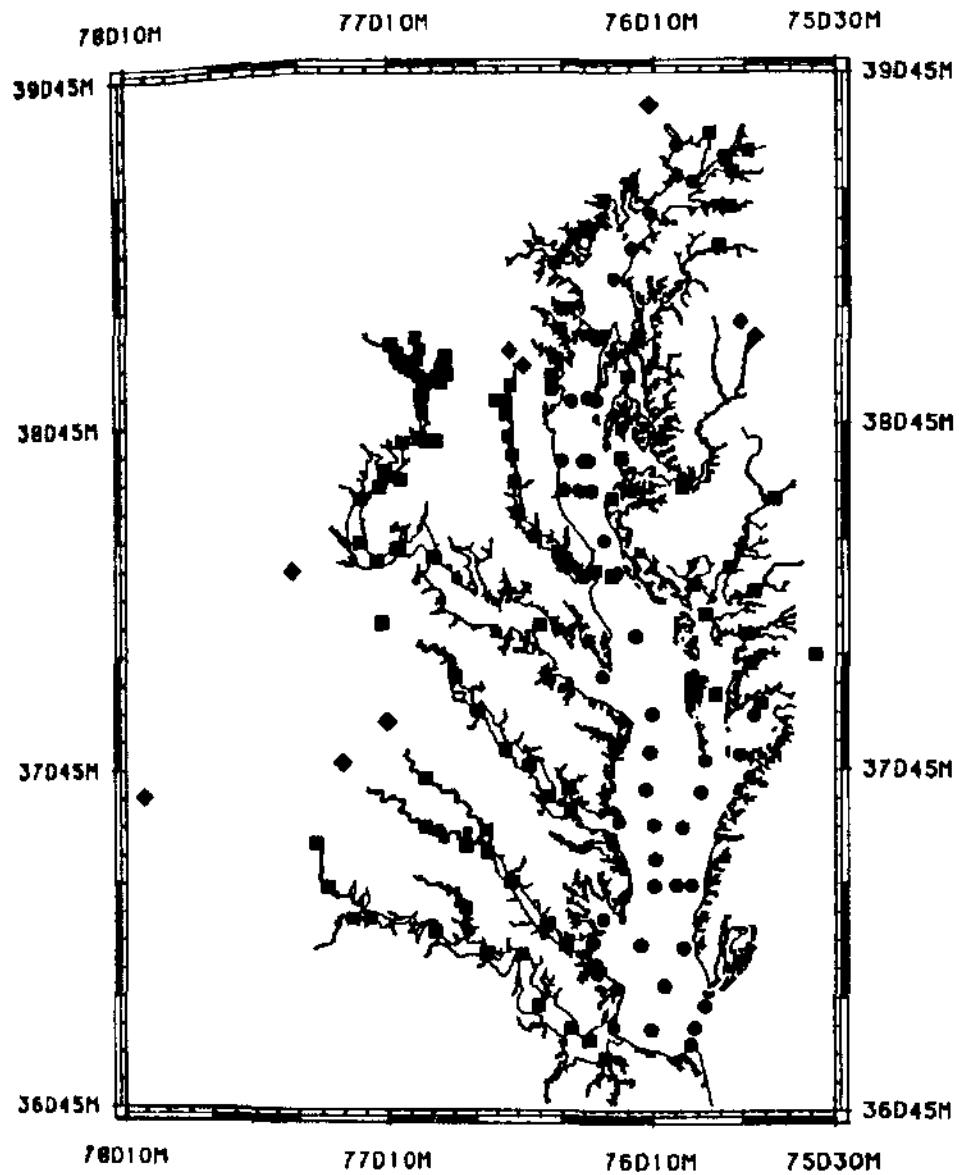
Figure 1. Maryland, Virginia and D.C. mainstem, tributary and fall line water quality monitoring stations.

HYPOXIA IN CHESAPEAKE BAY: RESULTS FROM THE MARYLAND OFFICE OF ENVIRONMENTAL PROGRAMS' WATER QUALITY MONITORING, 1984 - 1986

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The Maryland Office of Environmental Programs initiated a multidisciplinary, long-term water quality monitoring program in June, 1984 that encompassed Maryland's tidal tributaries and mainstem of the Chesapeake Bay. Several large scale, seasonal features concerning deepwater hypoxia were evident from the monitoring data as well as observations indicating that significant changes in oxygen concentrations were occurring on time scales of hours to days. Despite the fact that the relatively rapid changes in Chesapeake Bay hypoxia were not completely resolvable by this monitoring program which samples twice-monthly, strong inferences could be drawn about the associated processes.

Development of hypoxia was rapid in the spring of each year as dissolved oxygen levels generally declined to less than 1 mg/l by June in the upper deep trough region. The upper deep trough exhibits the most severe hypoxic/anoxic conditions with onset and dissipation of the problem occurring in this area first and last, respectively, relative to lower mainstem areas south of the Patuxent River. During the high flow summer of 1984, hypoxic waters of less than 1 mg/l extended well into Virginia mainstem waters while in 1985 and 1986 the affected zone was more restricted to Maryland waters. Strong mixing usually occurred in September, dissipating hypoxic conditions. In the October through November period of 1984 - 1986, dissolved oxygen concentrations declined once again by one to several parts per million from earlier levels before increasing again during the winter. These autumn dissolved oxygen declines

resulted in transient levels as low as 2 mg/l in bottom waters.

Dissolved oxygen concentrations in deep-trough mainstem bottom waters were quite variable although generally below 2 mg/l from June through early September. Physical processes apparently dominated the short-term changes in dissolved oxygen concentrations. The degree of stratification in the deep trough region, as measured by the change in density from surface to bottom, was particularly variable from cruise to cruise through the course of each year, although generally higher in spring and summer. Spring and summer of 1984 exhibited the highest sustained density stratification observed since 1983. The relatively rapid changes occurring in the physical structure of the water column are indicative of changes of freshwater input and vertical mixing.

The monitoring program was also able to document some important processes occurring in the lateral or cross-Bay direction. A major reaeration event was observed in the upper deep-trough during a cruise on July 10 - 11, 1984. Combining information on dissolved oxygen, salinity, density and nutrient concentrations in the vertical, lateral and longitudinal dimensions with local wind records, it was possible to evaluate hypotheses concerning the source of the dissolved oxygen to sub-pycnocline waters in all three dimensions. This evaluation led to the conclusion that north to northeasterly winds caused the pycnocline to tilt upward on the Eastern Shore bringing sub-pycnocline waters sufficiently close to the surface to become reaerated. A subsequent shift in winds to a southwesterly direction brought the newly reoxygenated waters (3-4 mg/l) into the mid-channel as the pycnocline tilt reversed. The lowest dissolved oxygen concentrations in sub-pycnocline waters were advected to the western shore. Thus, reaeration occurred without destratification.

Additional evidence for the importance of lateral processes came from dissolved oxygen measurements in embayments and lower tributary areas. These regions experienced occasional intrusions of high salinity, low

dissolved oxygen waters from the mainstem. These events are almost certainly the result of wind-driven tilting of the pycnocline that permits sub-pycnocline waters from the mainstem to intrude over the sills that are typically found at mainstem-tributary boundaries. In one case, an intrusion was observed as far upstream as Cambridge on the Choptank River.

An important seasonal feature in the onset of hypoxia was a large pool of algal biomass that developed from December to May of each year in bottom waters of the deep trough region. This pool reached typical concentrations of over 30 µg/l of active chlorophyll a through extensive reaches of the mainstem along with similar concentrations of pheophytin a. Results from the phytoplankton and processes components of the monitoring program shed some additional light on the accumulation of high algal biomass. Diatoms were an important part of the phytoplankton community during winter and spring. Sediment trap data indicated that this same period was characterized by higher proportions of primary production reaching bottom waters when compared to summer months. These settling algal cells were probably able to survive for extended periods below the euphotic zone in winter and early spring because of low temperatures and high oxygen levels. In May, this algal pool rapidly diminished coincident with the greatest decreases in bottom water dissolved oxygen. Thus, it is likely that the decomposition of late winter and spring phytoplankton growth that has settled to bottom waters and sediments, coupled with spring increases in stratification and temperatures, is a major contributor to the establishment of hypoxia in the deep trough region. Similarly, phytoplankton blooms in October, with diatoms again an important part of the community, may be an important cause of the transient decreases in oxygen levels observed in the fall.

DISCUSSION

Newell: We've heard a lot of presentations which refer to mg/l oxygen, while some have presented data which refer to "corrected" mg/l oxygen. I'm not sure what is meant by that. Since total mg/l of oxygen does change with temperature, surely a better way than absolute concentration is percent saturation because DO differences between different river systems could be just due to temperature differences. What does the audience feel about this?

Magnien: Corrected mg/l means it's corrected for salinity and temperature. Some of the field instruments do not correct automatically for these. Certainly the temperature patterns tend to reinforce low dissolved oxygen patterns that we see.

Haas: In the York River, the longitudinal temperature gradient from the mouth to West Point is less than $1^{\circ}C$. Vertically, in the summer, there is not that much difference. I don't think the temperature gradient is a very high magnitude. I don't know how much effect that would have on DO -- probably very little.

Mountford: I have a concern with using percent saturation in this context because we've done some exercises in the past and when you start getting a lot of photosynthetic activity, the oxygen values are sometimes well over 100% saturation. You start getting excursions that are related to biological activity in the water column that are hard to interpret and would end up confusing the picture more than clarifying it.

Newell: Do you see some DO values more than fully saturated?

Mountford: Correct -- we might see 115% or more.

Newell: I would think that using percent saturation would indicate whether the water was supersaturated more easily, wouldn't it?

Mountford: One could draw a line of temperature on most of those graphics we've seen and approximate what the saturation is.

(To Magnien): How much of sigma t is due to temperature? Would you do just as well putting salinity in?

Magnien: Salinity definitely drives sigma t. The greatest contribution of temperature to the density gradient would be in spring and during fall temperature changes. In spring, it is going to reinforce stratification with surface waters warming up more quickly than bottom waters; and in fall, the lower temperatures at surface relative to the bottom may be contributing to mixing that we see in September.

Tuttle: I have heard this word "anoxia" over and over again -- how do you actually know that you have anoxia when you say you do?

Magnien: I believe that our measurements are probably good to + or - 0.2 mg/l. With any current instrumentation for measuring DO it's probably as good as you can get. Even with Winklers, there is a problem of getting a sample up without having oxygen get into it. I think the question of whether you have anoxia versus 0.1 or 0.2 mg/l is worthy of addressing.

Tuttle: There may be an easy way of doing this . . . . When you have anoxia, you almost always have hydrogen sulfide in the water column. Simply measure hydrogen sulfide, then you know you have anoxia. Measuring it is pretty easy.

Magnien: Right, we have been experimenting with measuring hydrogen sulfide. But we also have to realize that we might have anoxia without hydrogen sulfide.

Tuttle: In absence of hydrogen sulfide, the CBI Winkler titration works quite well. As a matter of fact, Jay Taft at

CBI refused to use an oxygen meter below about 0.5 mg/l because he flat out did not believe the data.

Magnien: There are arguments both ways: one could say measuring DO in situ has an advantage because you're not risking contamination of the samples. With the Winkler technique, you have to bring a sample up and we found when you use a water bottle or pump -- any method -- it is going to risk contamination. I think that's essentially the problem.

Tuttle: There was a study done in the Black Sea in 1969 evaluating these things. If you use a Niskin bottle, the loss of hydrogen sulfide is quite minimal and if you haven't got hydrogen sulfide, oxygen doesn't change. So there are oceanographic confirmations of sampling techniques.

Jordan: For the large scale processes and even for ammonium and phosphate flux, does it really matter whether we know if it is zero?

Tuttle: It certainly does to the animals.

Jonas: I think we're going to see later on today, with regard to microheterotrophs, there is a very substantial difference between 0.5 mg/l of oxygen in the water column and zero oxygen. Zero oxygen means a lot to trophic dynamics, particularly in regard to microheterotrophs, and in the types of metabolic activities that are going to go on. Probably more redox potential phenomena than oxygen per se, but it will make substantial differences.

We can make a big case about a little bit of oxygen and zero oxygen -- crabs may not go there in any event, but as far as dynamics driving the system, it will be important. Therefore, measuring and confirming this anoxia is very important.

Tuttle: We've seen some interesting data here concerning oxygen dynamics. Going back to the 1950s, there is an enormous CBI data set. Could we not have figured out the same dynamics from the 1950's information instead?

Question: How many cruises were in a given year in the 1950s?

Magnien: My impression is that, in a given year, you're probably limited to 2 or 3 cruises, so the resolution wouldn't be too good.

Tuttle: My other question is that after hearing all this, is the hypoxia situation getting worse or is it getting better? Furthermore, haven't the physical conditions been the same for at least the last half a century?

Magnien: Certainly we're addressing the historical perspective in the next couple of years. EPA did it, Taft did it a number of years ago. We want to revisit that, use some more data, put together a picture of the historical record as best we can. We want to do it carefully because of all the problems that have been raised here. Certainly, factoring out physical factors would be a critical element. Maybe the pattern will be so strong it will overwhelm the physical dynamics, though that remains to be seen.

Haas: In that regard we've seen a lot about the different flow conditions in 1984 and 1985 and the effect on vertical stratification. In the York River at VIMS we do plankton monitoring, which is in the vicinity of the deep hole in the lower river where we have oxygen problems. During April and May, 1984, the salinities were 10-12 ppt and we had consistently over 50 μg/l of chlorophyll in the water column in that vicinity. In 1985, at the same period, with salinity at 18-20 ppt, there was no spring bloom. Unfortunately, I don't have the oxygen data to say that those differences in production really resulted in differences in oxygen in the deep river. Is somebody going to say that for the Bay? When you have these big differences in flow conditions which resulted in different amounts of stratification, did they in fact result in different production conditions for the spring bloom or is the Bay so big that the spring bloom in a high flow year is further down Bay but still impacting the main part of the Bay? Are the differences in 1984 and 1985 DO due to a greater degree of stratification from the high flow in 1984? This seems a critical question in trying to sort this out.

Sellner: Larry, we don't have primary production data from early 1984 -- our part of the program didn't start until August of 1984, so we just have the high summer production period. We have August 1984 on but we missed the critical spring bloom of 1984.

Fisher: A comment on the "spring bloom" we've been hearing about. Productivity increases from winter through summer, and drops off again. There is no particularly well-defined spring bloom like we see in a lake or ocean. Highest productivities occur in warmest months. The slide that Rob Magnien showed illustrated that. If you're talking about settlement of fecal materials, maybe a spring pulse of that secondary productivity in surface water is feeding a maximum summer oxygen demand.

Haas: Rates of production will be highest in the summer when light and temperature are the highest. What I think Bob is getting at is that the spring bloom may not be a "bloom" of production, but an accumulation of biomass because we're talking about large diatoms that aren't grazed much by zooplankton; that's probably the reason settling out is so great. High production in summer is mostly small flagellates that are grazed in the microbial food web and they probably don't settle out as much.

But there is certainly a tremendous peak of phytoplankton biomass in the lower York River in springtime. This may not be associated with a higher rate of production per se, maybe just an absence of grazing pressure which results in greater accumulation of biomass. Certainly, the highest sustained levels of biomass throughout the year occurring in the lower Bay and the tributaries of the lower Bay are in spring, where chlorophyll levels are five times higher than they are during the rest of the year.

Fisher: That may be the result of shifting patterns of where the chlorophyll maximum is. It may be pushed downstream and then move back upstream in response to flow.

Haas: That's a possibility. But even in summertime, the highest accumulations of biomass are still in the frontal

regions set up between the rivers and Bay. I think there is a pulse of biomass available for settling out in spring that is not available in the summer.

Fisher: I just wanted to raise the issue of productivity versus material settling out.

Haas: Right, that's a good point.

Comment: Some decomposition work I did on freshly settled particulates showed dramatically higher rates of decomposition in May. The only thing that was associated as far as I could tell was not necessarily a bloom but very high percentages of organic matter in the suspended material which was presumably settling out. And the oxygen consumption rates were dramatically higher than any other time of year.

Magnien: One other point I wanted to make is that most of this material accumulating in bottom waters during late winter and spring is living, which indicates it's probably fairly labile. It may be important that in the spring the carbon making it down is "ready to process" and that it's a bit more refractory at other times of the year.

Jonas: All of the Bay literature with regard to organic demand on oxygen centers on particulates. Last year during the 1985 season, we were able to run engineering-type biochemical oxygen demands on both unfiltered and filtered water samples, filtered with GF/F glass fiber filters. There actually is a shift over the season from the dominant labile pool being particulate earlier on, to being what we'll call "dissolved" for the moment and which passes a GF/F filter. So there is a shift, and the full oxygen demand may be shifting over to the dissolved portion. That's simply being missed when you look at particulate settling rates.

Comment: I saw that, too.

Mountford: Bob, does that mean maybe we should do something like BODs in monitoring?

Jonas: I wouldn't argue against that. It's a simple technique based in engineering. The problem, like the oxygen one, is that unless you are very careful, the variance in the technique will leave you with oxygen values all over the place. It's one of those things that requires hand manipulation and great care, because we're looking at sometimes only 1.0 mg/l total demand on a particular sample and that means a 5-day incubation in the dark and there are a lot of logistical problems. Whether or not the big monitoring effort can handle that, well, my argument is that there is no good substitute or alternative unless you want to go to the extent of measuring total carbohydrate or amino acids. Maybe analytically, if one were tooled up to do that, that would be cheaper and easier in the long run.

Ducklow: If you want the simplest technique to address that question, just count bacteria. It is precise, very easy and you can put them away and do them later. And it correlates with all that stuff.

Mountford: The question that Larry asked is seminal to the whole thing. He was talking about whether production in 1984 and 1985 were measurably different. Rob Magnien may second this or argue with it, but scanning the surface chlorophyll data I see no such pattern between the two years; but in thinking back on the figure that Rob showed of bottom chlorophyll, I wonder if you could do a mass comparison over those two years and get a feeling for whether the subpycnoclinal chlorophylls were different from one year to another. It could be worth looking at.

Sellner: We do have that data; it is in our report. Getting back to this whole question and the point that Tom brought up -- if you look at standing crop, not production, there are two distinct peaks: one that Rob had as his bottom chlorophyll that is principally the Prorocentrum recirculation phenomenon that Mary Tyler and Howard Seliger talked about some time ago, and also diatoms. If you look at depth-integrated chlorophyll, they are higher in the winter than in summertime. So in fact the standing crops are higher at that time, and if you look at species composition of the phytoplankton, the bottom chlorophyll is principally the large

shelf-type diatom assemblages. Then as you shift from summer to the late fall peak that Rob refers to, there is another diatom pulse that is not shelf-related, but is truly estuarine. But there are two distinct standing crop peaks: The one in late winter-early spring is principally diatoms and Prorocentrum-like cells, and then the October peak is diatoms.

Malone: I don't think you can say a lot about productivity based on chlorophyll. The interannual variations in summer production are pretty clear. The productivity in the summer of 1984 was much higher than in the summer of 1985. Both seasonal and interannual variations in production in the water column and oxygen demand compared quite well.

I'd like to get back to the original (monitoring) data. I am just overwhelmed by the richness of that data. The question I really have is, do you think the size of this program will affect how long you will be able to run it? And if so, are there any plans to objectively scale down the program so that it will provide you with consistent information, but over a longer period of time?

Batiuk: I would answer that with a question: How many years of data do we need to take a look at the current structure of the mainstem and tributary program, and then to go about reevaluating to say we can drop this station and keep these others? We've been going back and forth in terms of getting an agreement, and talking about what the feds will put in and what states will take in over the long run. We would like to keep it as it is -- a lot of people say it is a minimum -- but you have to be realistic that you may not be able to sustain something this large. But we would want to keep it for a good couple of years or more so we can make some careful scientific judgments on keeping different stations. That is, keep it as it is as long as we can, and then when we are more comfortable, pull back a bit and perhaps supplement with remote sensing, e.g., buoys on lateral stations, or try and supplement it in some other ways. I would not like us to see us chop it up next year, for example. We'll try to develop a scientific basis to make management decisions on the program. I would like to see it go 10 or 20 years, but we have to be realistic.

We don't have enough data to say what stations are or are not useful now. That's the kind of give and take we need from the scientific community, from people that are using the data. We may need to emphasize some areas, and there may be areas we can pull back.

Jordan: This monitoring program may seem expensive -- but compared to resources that are ultimately going to be put into restoration of the Bay, it is a drop in the bucket. So the financial considerations may not be so critical.

Malone: I don't see that you can maintain a monitoring program of this size for a decade or two. A long-term time series is a lot more important in the long run than high resolution spatial coverage, for example. There are a lot of reasons for not being able to maintain it forever. Energy, for one.

Magnien: When you get into the details, you see that there is sometimes an economy of scale. You say, "we'll do half as many stations," but in reality when you get the boat out there and you have to cover the same distance, what's the incremental cost of taking another DO profile and taking samples?

In certain aspects, we may have too much detail, and in other aspects there may be parameters we're missing. I think we probably have pretty reasonable coverage. This doesn't mean we can't continue to evaluate and maybe scale back certain aspects or expand others. I would also agree with Steve's point -- I don't think we're over-resolving the system so that we know everything that is going on all the time. Many aspects of the program are not as intensive as the chemical suite of stations that represents sort of a "backbone." But when you look at plankton, there are only 16 stations and only one station where vertical flux measurements are taken. Some aspects of the program we've scaled back initially because of cost. We're hoping that the "backbone" will be a way of interpolating some of the reduced subset of measurements, along with the research projects, of course, so we can get more of a complete picture. Again, costs may seem large in terms of

research grants, but look at the resources being expended on the Bay in Pennsylvania, Maryland and Virginia. We're making progress and it seems like a worthy investment to ensure that we're on track and continue on track.

Summers: At least for the present. Since I've been at OEP for three years, monitoring really has taken off. We have this big program, and we still have people from counties with more localized concerns coming in saying "this is too broad; we can't do anything with it," and so they're actually funding additional monitoring on top of this at a higher level of detail. So it is still growing, it hasn't gotten scaled back.

Dissolved Oxygen Processes

NEAP-SPRING TIDAL EFFECTS ON DISSOLVED OXYGEN AND RIVER-BAY INTERACTIONS IN THE LOWER YORK RIVER

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It is now well established that the lower York River undergoes a predictable and persistent oscillation between vertical density stratification and homogeneity in close association, respectively, with neap and spring tides (Haas, 1977; Hayward et al., 1986). Wind and mean sea level play a minor role in regulating this phenomenon and freshwater river flow appears to have no effect on this process (Hayward et al., 1986). The portion of the York River which undergoes this oscillation is also subject to chronic seasonal hypoxia stress, which is usually first apparent in May, most severe in August and dissipates in September (Jordan, 1974). In the one instance in which the effect of the fortnightly tides on the vertical distribution of dissolved oxygen was examined, it was observed that destratification resulted in an increase in bottom water oxygen from about 0.5 mg/l to about 4 mg/l in a maximum of five days. The rapid subsequent restratification of the lower river was coincident with a decrease in bottom water oxygen to less than 1 mg/l (Webb and D'Elia, 1980; D'Elia et al., 1981).

In addition to a direct effect on the vertical distribution of dissolved oxygen in the lower York River, the process of a fortnightly, tidally-driven, density gradient oscillation also illustrates the close hydrographic coupling between the lower York and the Chesapeake Bay. The onset of spring tide destratification is triggered by an influx of less saline water from the Bay into the lower York. This water originates upbay and is advected into the river as a result of a tidal phase shift in which flood tide in the river

mouth is coincident with the end of ebb tide in the Bay. During spring tides this influx of less saline water to the lower river is enhanced and causes a reversal in the longitudinal salinity gradient in the lower river, which diminishes gravitational circulation and allows spring tidal mixing processes to reduce vertical density stratification (Hayward et al., 1982). The restratification of the lower river following spring tides results from the rapid advection of high salinity water from the Chesapeake Bay along the bottom of the lower York River (Ruzecki and Evans, 1986). Thus, both destratification and restratification in the lower York River are regulated by hydrographic processes occurring between the river and the Bay, not by processes occurring upriver.

The significance of these observations related to hypoxia processes in the Chesapeake Bay is that within the widely recognized seasonal cycle of hypoxia, significant short term alterations in dissolved oxygen do occur. At present, it is not clear to what extent this density oscillation and possible effects on dissolved oxygen distributions occur in the lower Rappahannock and James rivers or the lower Chesapeake Bay, but one should be cognizant of the possbility of short term variation in deep water dissolved oxygen concentrations. Furthermore, these observations illustrate the close hydrographic association of lower river-Chesapeake Bay processes. In Virginia, chronic hypoxia in the York and Rappahannock rivers is restricted largely to the lower portions of each of these rivers, and the possibility that hypoxia is affected by Chesapeake Bay processes or conditions should not be ignored.

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INTRUSION OF LOW DISSOLVED OXYGEN WATER INTO THE CHOPTANK RIVER

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One aspect of the apparent increase in the persistence and extent of low dissolved oxygen (DO) in the deep meso-haline Chesapeake Bay over the last 30-40 years has been an apparent increase in low DO in adjoining tributary estuaries. The cause of low DO in the deeper waters of these tributaries is not fully understood. One hypothesis is that it results from local processes, i.e., the same processes responsible for low DO in the mainstem lead to the formation of pockets of low DO in tributaries. Alternatively, Seliger et al. (1985), have suggested that DO effectively acts as a tracer for the deep water of the mainstem, and is advected directly into tributaries under the proper conditions.

The Choptank River estuary is an example of a commercially productive tributary that may be impacted by episodes of low DO. Previous measurements of hypoxic or anoxic conditions in the Choptank, however, have been too spatially limited and too infrequent to adequately establish the extent, duration or source of the low DO. To better address these questions, the Maryland Department of Natural Resources and Horn Point Environmental Laboratories carried out a joint research study during summer 1986, incorporating both a water quality monitoring effort throughout the lower Choptank at roughly weekly intervals and a program of moored observations in the Choptank entrance channel. This presentation is a description of the preliminary results of that investigation.

The study's primary hypothesis is that intrusions of low DO from the lower layer of the Chesapeake Bay occur

during episodic, wind driven surges of lower layer water into the Choptank. Steady advection of low DO by the density driven estuarine circulation is not as likely. This hypothesis is based on the previous work of Ward and Twilley (1986), who only measured low DO on the bayward side of the broad, shallow sill at the mouth of the Choptank; on the work of Boicourt et al. (personal communication), who showed the lower Choptank to be strongly wind forced; and on simple considerations of the topography of the lower Choptank. Lower layer water from the mainstem of the Bay can only reach the Choptank through the old entrance channel, bounded on the Northwest side by Sharps Island Bar and on the Southeast by the neck district of Dorchester County. The channel depth varies between 10 and 20 m, and the channel is about 15 km long. The sill at the mouth of the Choptank is at the head of the channel, and at 8 m depth is shallower than the mean depth of the summertime pycnocline in the mainstem. Surges of lower layer water up the entrance channel might be forced by some combination of local wind driving and the remotely forced cross-Bay pycnocline tilting events reported by Malone et al. (1986). Tidal mixing is presumably much stronger on the sill than it is in the entrance channel; thus, low DO is more likely to persist longer and affect a greater portion of the river during a surge than it is during steady, slow advection.

Moored observations were made at three stations: one at the outer end of the Choptank entrance channel, one at the inner end just bayward of the sill, and one on top of the sill south of Broad Creek. Current speed and direction, temperature and conductivity were measured at all stations. In addition, an attempt was made to obtain long time series of near bottom DO at the inner two stations, using new Endeco Pulsed DO sensors. The water quality monitoring program covered the entire lower Choptank from the Cambridge bridge to the outer end of the entrance channel with 26 stations.

Preliminary results indicate that our primary hypothesis is correct, with the caveat that 1986 was the lowest river flow year in the last seven for the Choptank drainage basin (T. Fisher, personal communication), so that the density

driven circulation was weak. Results of the monitoring program show that DO is highly variable near the mouth o the river; near bottom DO on the Bayward side of the sil changed by as much as 6 mg/1 over a one-week interval The two time series of DO obtained from the mooring on the sill, though limited in extent, also show a great deal o variability, with near-bottom DO levels changing by almos 6 mg/1 in 6 h. During apparent intrusion events, characterized by hypoxic water up the entrance channel and slightly over the sill, DO was highly spatially conservative with salt, indicating advection from the Bay. This conservative behavior of DO with salt also is apparent in the time series of near bottom DO from the sill mooring. Advected hypoxia was apparently confined to the immediate vicinity of the mouth of the river, however, and to depths greater than about 5 m. In contrast to the behavior of hypoxia near the mouth of the river, an area of near bottom hypoxia in the deep water near Castle Haven was fairly constant, and possibly can be attributed to local processes.

A tentative model for advective surges of low DO near the mouth of the river is of 1-2 day intrusion events followed by 3-4 day mixing and reaeration periods. The surges are clearly related to the wind, but depend in a complex manner on wind direction and on the pattern of wind variability. Further analysis of existing data and more observations during 1987 should help to answer remaining questions and provide a complementary view during a higher river flow year.

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DISCUSSION

Mackiernan: Do you feel that the York is unique since it has a relatively low freshwater flow in comparison with some of the other river systems? What are the other rivers like?

Haas: The James River seems to undergo the same sort of neap/spring oscillation, but a few years ago a more intensive survey indicated that it was not nearly as nice a picture. We made daily slack water runs for 14 days looking at this oscillation and while certain stations in the James River destratified during spring tides, an adjacent station wouldn't. So the hydrography of the James seems to be much more complex than the York River, but it goes along with the idea that the James River has much greater vertical salinity structure and maybe is more resistant to mixing than the York and Rappahannock. So I don't know the degree to which the Rappahannock and James respond to neap/spring tidal effects. This may indicate something about their hydrography that relates to the lack of low oxygen stress in the James River. Specifically about freshwater inflow, I don't know.

Question: What is the spatial extent of this oxygen problem in the lower York? Indirect evidence from looking at benthic communities, as we move up out of the channel area, shows that the community seems to be dominated by long-lived and deep-dwelling organisms. We've never seen oxygen problems up out of the channel, right off the pier.

Haas: In terms of longitudinal extent, how much of the river undergoes this oscillation is in the article by John Ruzecki that looks at longitudinal impact of the neap/spring tidal effects. The answer to your question about depths affected is most of the impact of low dissolved oxygen is below 7 or 8 meters, which is the normal depth of the pycnocline, when it is stratified. So water depths less than that appear not to be impacted by low oxygen.

Mountford: It seems as you move up the Bay maybe tidal amplitude is enough to drive the spring and neap mechanisms — Chris D'Elia looked at it in the Patuxent and found it kind of ephemeral. What do you think about the Potomac, where USGS did a lot of work. Does it happen there?

Haas: I have some information from USGS -- I'm not sure if it's actual data or from a model -- but it seems to suggest that certain parts of the Potomac undergo this oscillation. The York River seems to be the one river where it is well documented in time and space. The James, Rappahannock, Potomac and maybe the Patuxent give indications that sometimes it might be an influence. It is something you have to keep in mind in your sampling program and look out for from a practical point of view when you're studying these kinds of vertical processes.

Boicourt: I can back this up, although I will disagree with that particular model because it was run on the hydraulic model at Mattapeake, which is not an appropriate way of looking at vertical mixing; however, the neap/spring variations we see in the Bay proper and the Potomac are reduced for the reasons that Larry Haas has talked about and reduced over what we see in the lower Bay tributaries

Mountford: Is this, then, a nutrient pump that has some sort of frequency of moving material up into surface layers? Does it affect phytoplankton standing crop?

Boicourt: Probably not in the Bay proper.

Haas: While nutrient concentrations look very high in the deep water, if you look at the cross-sectional area, it's a relatively small volume of deep water compared with the cross-sectional area above the pycnocline and so there is a tremendous dilution effect when you mix the bottom water up. Mixing appears conservative; in other words you have just as much material per unit area through the water column before and after mixing, so there is a large dilution effect. So the impact of the nutrients may not be that great on the surface water. Probably farther up the tributaries you don't have such high concentrations in the deep

water as you do downstream; the dilution effect would be less as you go up river.

Kemp: I'm not sure if we should leave this issue with that final statement, because I think there are indications that there is some impact. It's pretty fuzzy at this stage, and maybe Tom should comment on this but, after tilting events (for example in 1984 when we had a pretty good data set), there is an indication of increased chlorophyll in the flanks -- in shallow stations to the side of the channel. But you have to use a time lag, and I don't know what the appropriate time lag is. Clearly, the concentrations of nutrients in the shoal water are substantial following such events.

Malone: One of the puzzling things we ran into is that while increases in chlorophyll appear to be related to nutrient supply, nutrients are rarely exhausted and usually occur at concentrations that probably do not limit growth rate.

Haas: The whole time that that 1982 data set was taken for salinity at the Coast Guard pier, we also took chlorophyll and cell count data with the express purpose of linking up phytoplankton dynamics with physical dynamics. I was hoping the relationship would be so dramatic it would hit me over the head. But it takes a lot of work to get the signal out and that's why it isn't published yet. There may be an influence and there may not be -- but it is certainly not dramatic.

PHOSPHORUS CYCLING AND NUTRIENT LIMITATION IN THE PATUXENT RIVER

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No single issue in the Chesapeake Bay region has focused the attention of the public, federal and state management agencies and elected officials more than excessive nutrient enrichment and its consequences. Sea Grant's present interest in the study of hypoxia relates directly to this issue, although in the eyes of the public especially, the conceptual link between nutrient enrichment and hypoxia is unclear. The present abstract considers this relationship and the relevance of some ongoing research and monitoring efforts.

Interest in the nutrient enrichment problem has typically centered on the freshwater portions of the tributaries. For example, the Potomac clean-up effort has attempted, with a disputed degree of success, to reduce algal biomass and the presence of noxious cyanobacteria in the region just south of the Washington metropolitan area.

As concern has shifted to the problem of hypoxia in the lower reaches of western shore tributaries and in the mainstem of the bay, so too has interest shifted to understanding possible anthropogenic factors that cause it. In the eyes of some managers, the transport of allocthonous oxygen-demanding material to the saline portions of the estuary is at fault. To them, the obvious solution is to reduce discharges with high BOD and to establish nutrient reduction strategies aimed at controlling the growth of algae in freshwater areas of the tributaries. The nutrient reduction strategy of choice of freshwater areas has traditionally been based on phosphorus removal at sewage treatment plants.

Many in the scientific community have argued instead that while such steps may be necessary, they are not sufficient for dealing with the degradation of saline areas: only autochthonous primary production in these areas is capable of producing sufficient organic matter to be responsible for oxygen consumption in the deep waters of the estuary. Accordingly, steps must be taken to understand nutrient limitation and dynamics in these areas.

The Patuxent River is a convenient model subsystem to study enrichment effects for a variety of reasons: (1) it is well-studied historically and is believed to be exhibiting signs of more severe hypoxia in the last several decades; (2) its size makes it relatively easy to sample; (3) it is located in the fast-growing area between Baltimore and Washington, and thus is receiving more point-source inputs; (4) good estimates of point and non-point source nutrient inputs are available; and (5) it is particularly accessible for study by scientists from both Chesapeake Biological Laboratory (CBL) and the Benedict Estuarine Research Laboratory (BERL), which are both situated on the estuary.

A joint study by BERL and CBL scientists, supported in part by Sea Grant, has shown that nitrogen is the key element that stimulates summertime autochthonous primary productivity in a section of the Patuxent just downstream of the turbidity maximum. If, in fact, summertime productivity is coupled closely with oxygen-demanding processes that contribute to hypoxia in the lower Patuxent, then a nitrogen-based nutrient strategy must be adopted to improve water quality. However, several important questions remain unanswered:

1. Can phosphorus be made limiting? Many contend that although P is not now limiting, a phosphorus strategy will reduce P levels enough to cause it to be. This should largely depend on the degree to which P is retained in the sediments of the estuary and is cycled within the water column. Historical evidence for many temperate estuaries suggests that sediment reserves of P elevate water column concentrations in the summer; this process appears to be stimulated by hypoxia. Thus,

feedback may exist in which the settling of particulate matter and associated BOD results in P enrichment of the water column. If a P strategy can limit productivity adequately to interrupt the feedback, it should be effective. Prediction of this will require (1) understanding of the relationship between primary productivity, sedimentation and benthic oxygen demand and nutrient regeneration, and (2) appropriate mathematical models and nutrient budgets (see below).

2. Are the kinetic equations used in models correct? Water quality models may provide projections of future autochthonous productivity and oxygen concentrations in the estuary. However, kinetic coefficients now used have largely been derived from work with marine and freshwater phytoplankton. Do estuarine species behave similarly? My Sea Grant project is aimed at determining not only phosphate uptake and growth co-efficients for estuarine phytoplankton, under different conditions of nutrient limitation, but also to establish the rates at which P cycles in the water column. This information should be useful for modeling.

3. Are present capabilities for developing nutrient budgets for the Chesapeake and its tributaries adequate? If so, what can we learn from nutrient budgets that has bearing on management issues? There is a wealth of data available on nutrient standing stocks and transformations; however, much of the data is unsuitable for adequate budgetary work. Inadequate precision or inappropriate methodologies have been employed that make mass balance estimates impossible. For example, in saline regions of the Chesapeake, the precision used in many sampling programs has resulted in reports of "not detectable" for phosphate and ammonia for large periods of the year. Although the standing stocks of these nutrients may be low, the volumes of water are so large that the mass (volume x concentration) of N or P involved is enormous.

I hypothesize that when adequate budgets become available, we will find that the nitrogen budget is a rather

"open" one and the phosphorus budget is rather "closed." By this I mean, that much of the N entering the estuary is removed by denitrification and is not retained in the eco- system. P, on the other hand, is conserved in the ecosystem in sediment reservoirs. Unlike many ecosystems in which productivity is controlled by available phosphorus's regula- tion of nitrogen fixation, in the Chesapeake N fixation is trivial and denitrification plays a far greater role. The management ramification is obvious: nitrogen control may be necessary.

NUTRIENT CYCLING IN CHESAPEAKE BAY

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Concern over anoxia in Chesapeake Bay waters inevitably concerns nutrient supply. The current paradigm linking nutrients with anoxia is that an enhanced supply of nutrients stimulates algal growth and sedimentation of organics into deeper waters where respiration consumes a limited supply of oxygen. In order to understand the origins and control its occurrence, it is necessary to quantify the total supply of nutrients.

The availability of nutrients to phytoplankton in surface waters is the sum of both the new inputs and recycled N and P. Inputs result from rain and advective additions from the surrounding watershed, and nutrients are recycled as a result of sediment diagenesis and heterotrophic activity in the water column (Figure 1). The total supply of N and P is the sum of these processes, and the hypothesis to be tested in this research is that recycling in the water column is quantitatively the most important process of those listed above.

In order to test this hypothesis, direct measurements of water column recycling of N and P were conducted with $^{15}N-NH_4$ and $^{33}P-PO_4$. Both particulate and nutrient pools were removed in time series and analyzed for pool size (μM) and isotopic content. Isotope dilution of the ammonium and phosphate pools was used to compute rates of regeneration, and uptake was calculated from isotopic incorporation into the particulate pools. These measurements were made using samples of surface and bottom water obtained from the central part of the Chesapeake in May and August, 1986.

An example of the data obtained in this study is shown in the attached Figure 2. The ^{15}N in the ammonium pool was slowly diluted and appeared in the particulate N pool during the six hour incubation. In contrast, the soluble reactive phosphate pool (SRP) was rapidly diluted (note log scale on y axis and minute scale on x axis), and label appeared quickly in the particulate P pool. Uptake (U) and regeneration (R) were computed from the rates of change in the pools and are indicated in each panel in nmol/l/hr These data indicate that the ammonium and SRP pools were turning over on time scales of hours and minutes, respectively, and that P was cycling faster than N in relation to Redfield stoichiometry.

There were significant differences between the rates obtained at the two times of year and in surface and bottom waters. In general, turnover times were longer and rates of uptake and regeneration were lower in bottom waters than in surface waters. Nitrogen cycled more rapidly in summer than in winter, but phosphate exhibited the opposite. The ammonium pool turned over in about an hour in August, whereas the SRP pool had a turnover time of about 40 h (Table 1). These data are consistent with the concept that phosphorus is more limiting under spring, high runoff conditions, and nitrogen is more limiting under summer conditions. Two sets of data associated with a wind-driven overturn event in August have been excluded from this summary. In these samples, nutrient-rich bottom water was brought to the surface and turnover times were very long and rates of uptake and regeneration were low.

We have used the regeneration data to compute median values of the total heterotrophic supply of ammonium and phosphate in the water column. We assumed that the surface rates were representative of a 5 m surface mixed layer and that the bottom rates represented a 5 m bottom layer. The rates obtained ($mmol/m^2/d$) are shown in Table 2 along with data on new inputs and cycling of N and P via sediments. The latter two estimates were obtained from the 1982 EPA report on the Chesapeake. The data show that water column recycling is the largest source of N and

P, and emphasize the importance of recycling processes relative to inputs of new N and P. The data may also be used to compute the number of cycles that inputs of N and P undergo before export or burial (recycling/inputs). These data indicate that N and P inputs are recycled 30-120 times, mainly in the water column. This analysis supports the hypothesis given above, and suggest that a better understanding of the anoxia problem will be achieved when the total supply of nutrients is better quantified.

nutrient supply   ⟶   algal biomass
        ↑   ↓
        ↕ ?   ↕
        ↑   ↓
anoxia   ⟵   sedimentation

total nutrient supply   =   inputs + recycling

        inputs   =   rain + terrestrial (new)

    recycling   =   sediments + water column (reused)

Figure 1. Schematic diagram of nutrient cycling in Chesapeake Bay.
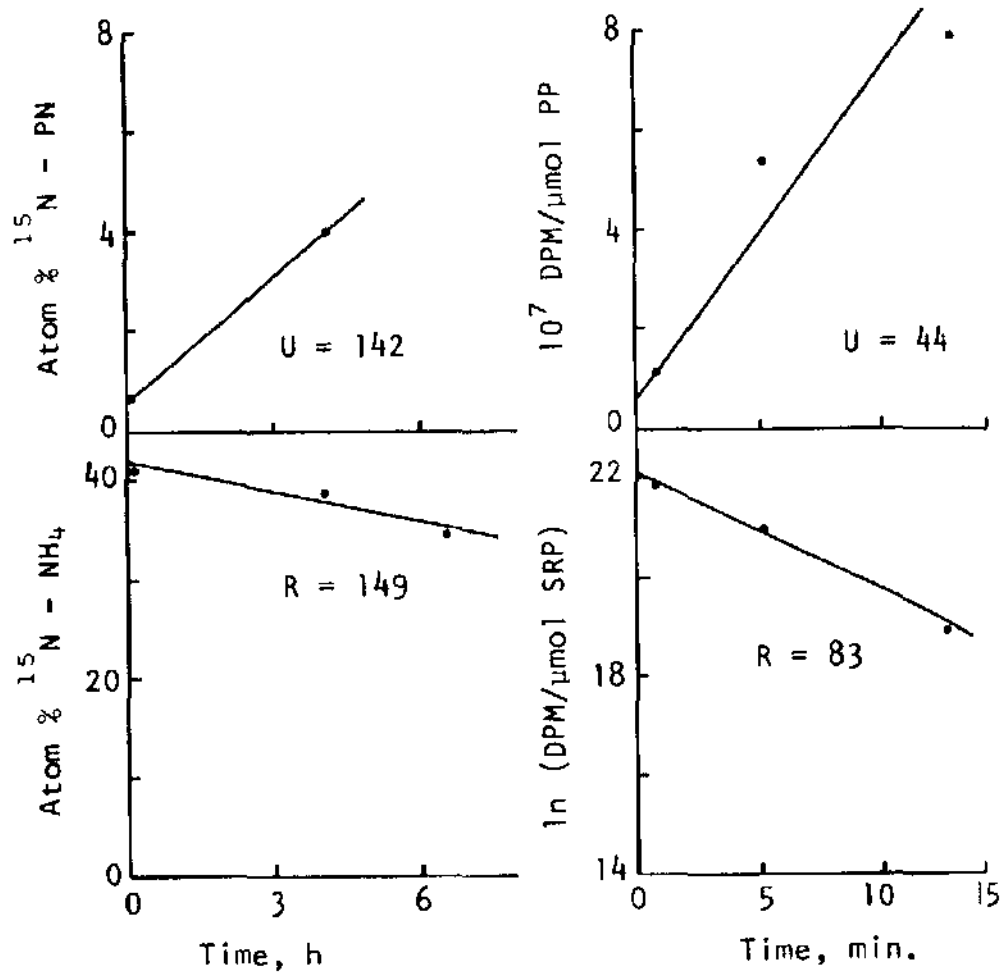
Figure 2. Rates of regeneration and uptake of ammonium, phosphate during a six-hour incubation using labeled ^{15}N-NH$_4$ and ^{33}P-PO$_4$.

Table 1. Turnover times for major nutrients in Chesapeake Bay in May and August 1986

	May 1986	August 1986
Ammonium (surface layer)	4-9 h	1 h
(bottom layer)	18-220 h	-
Particulate N (surface)	27-61 h	40 h
(bottom)	79-170 h	-
Phosphate (surface)	4-7 min	39-40 h
(bottom)	48-110 min	84-90 h
Particulate P (surface)	0.3-5.6 h	40-50 h
(bottom)	4-45 h	60-80 h

Table 2. Nutrient supply and recycling in Chesapeake Bay

	mmol/m2/d		% total supply		No. cycles	
	N	P	N	P	N	P
Water column	46.	9.0	78	95	22	112
Sediments	11.	0.43	18	4	5	6
Inputs	2.1	0.080	4	1	-	-
TOTAL SUPPLY	59.1	9.51	100	100	27	118

SEASONAL OXYGEN DEPLETION AND PHYTOPLANKTON PRODUCTION IN CHESAPEAKE BAY: PRELIMINARY RESULTS OF 1985-86 FIELD STUDIES

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The response of estuarine systems to nutrient enrichment is a major problem in marine ecology which has broad implications in terms of both water quality and fisheries. Nutrient enrichment from natural or anthropogenic sources can stimulate phytoplankton production, leading to increased fish yields or to decreased water quality. The degree to which one of these effects predominates over the other depends in part on the rates and pathways by which organic matter produced by phytoplankton is metabolized by heterotrophic components of the system. A critical factor here is the extent to which the photosynthetic production of organic matter is separated in time and space from the aerobic decomposition of this organic matter. In general, the more closely phytoplankton production and heterotrophic consumption are coupled, the lower the probability that increases in phytoplankton production will lead to a decline in water quality.

In Chesapeake Bay, it is generally assumed that increases in anthropogenic nutrient inputs have caused phytoplankton production to increase and that this increase has lead to a decline in water quality over the last 3-4 decades. An increase in the temporal and areal extent of oxygen depletion during the summer is believed to be one feature of this decline in water quality. This scenario has several weaknesses. (1) Cause-and-effect linkages between nutrient input, phytoplankton production, and increases in oxygen demand below the pycnocline have not been documented or quantified. (2) Inputs of new (allochthonous)

nutrients account for only about 10% of annual phytoplankton production so that a linear serial relationship between nutrient input and oxygen depletion is unlikely. That is, the fate of nutrient inputs depends more on system characteristics than on the magnitude of the input per se. (3) Finally, nutrient input and the fate of these nutrients depends to a great extent on fresh water runoff and wind-mixing, both of which exhibit large episodic, seasonal, and interannual variations. These variations modulate the patterns and rates of nutrient input and nutrient cycling within the Bay.

The dynamics of the production and fate of phytoplankton biomass is clearly of central importance to this issue. As a first step toward parameterizing the rates and pathways by which organic matter is metabolized, we must determine the time and space scales on which phytoplankton vary and how these variations are related to variations in nutrient supply and oxygen depletion.

The objective of this presentation is to describe temporal variations in phytoplankton biomass and their relationship to seasonal oxygen depletion of bottom water.

Data were collected at five stations along an east-west transect in the mid-Bay between the Choptank and Patuxent rivers (Figure 1). Flow of the Susquehana River is the major source of new nutrients and of buoyancy in the reach of the Bay. Vertical distributions of temperature, salinity, nitrate, nitrite, ammonium, phosphate, particulate organic carbon and nitrogen, chlorophyll, and dissolved oxygen were determined at 3-10 day intervals during summer 1984 and from February through September during 1985 and 1986. Phytoplankton production was determined at 7-10 day intervals.

Dissolved oxygen began to decline below the pycnocline in February as soon as temperature began to increase. The rate of decline was maximal during May and reached its seasonal minimum in August and July during 1985 and 1986, respectively (Figure 2). These cycles of dissolved oxygen did not appear to be related to variations in vertical stratification, but did appear to be related to variations in phytoplankton biomass. Seasonal cycles of chlorophyll a

(Chl) and Chl-specific phytoplankton production (P/Chl) were out of phase. Chl was highest during March-May when concentrations were high throughout the water column and P/Chl was low (Figure 3a). P/Chl was highest during June-August when Chl was low and concentrated in the surface layer (Figure 3b). Seasonal variations in Chl were directly related to seasonal variations in the volume transport of the Susquehanna, suggesting a relationship between nutrient input and accumulations of phytoplankton biomass on a seasonal time scale (Figure 4). Chl content of the water column decreased rapidly during May, primarily as a consequence of a rapid decline in Chl below the euphotic zone (and the pycnocline) which coincided with the rapid decrease in dissolved oxygen. These trends indicate that phytoplankton production and grazing are poorly coupled during spring and closely coupled during summer. Thus, there is a large build-up of phytoplankton biomass during March-April even though phytoplankton growth rate was low (on the order of 0.1/day).

The rapid decline in phytoplankton biomass in May could reflect an increase in mortality rate due to exposure to low oxygen concentration below the euphotic zone. Such an increase in mortality could cause a rapid increase in BOD leading to further reductions in dissolved oxygen. Thus, a positive feedback could develop between oxygen depletion and BOD as oxygen concentration declines. This could make the difference between hypoxia and anoxia. Simple mass balance calculations indicate that the magnitude of the spring accumulation of phytoplankton biomass could determine the extent of summer oxygen depletion. Since seasonal variations in Chl and river flow were correlated and fresh water runoff is the major source of new nutrients, this might be the critical link between nutrient input and oxygen depletion in Chesapeake Bay.
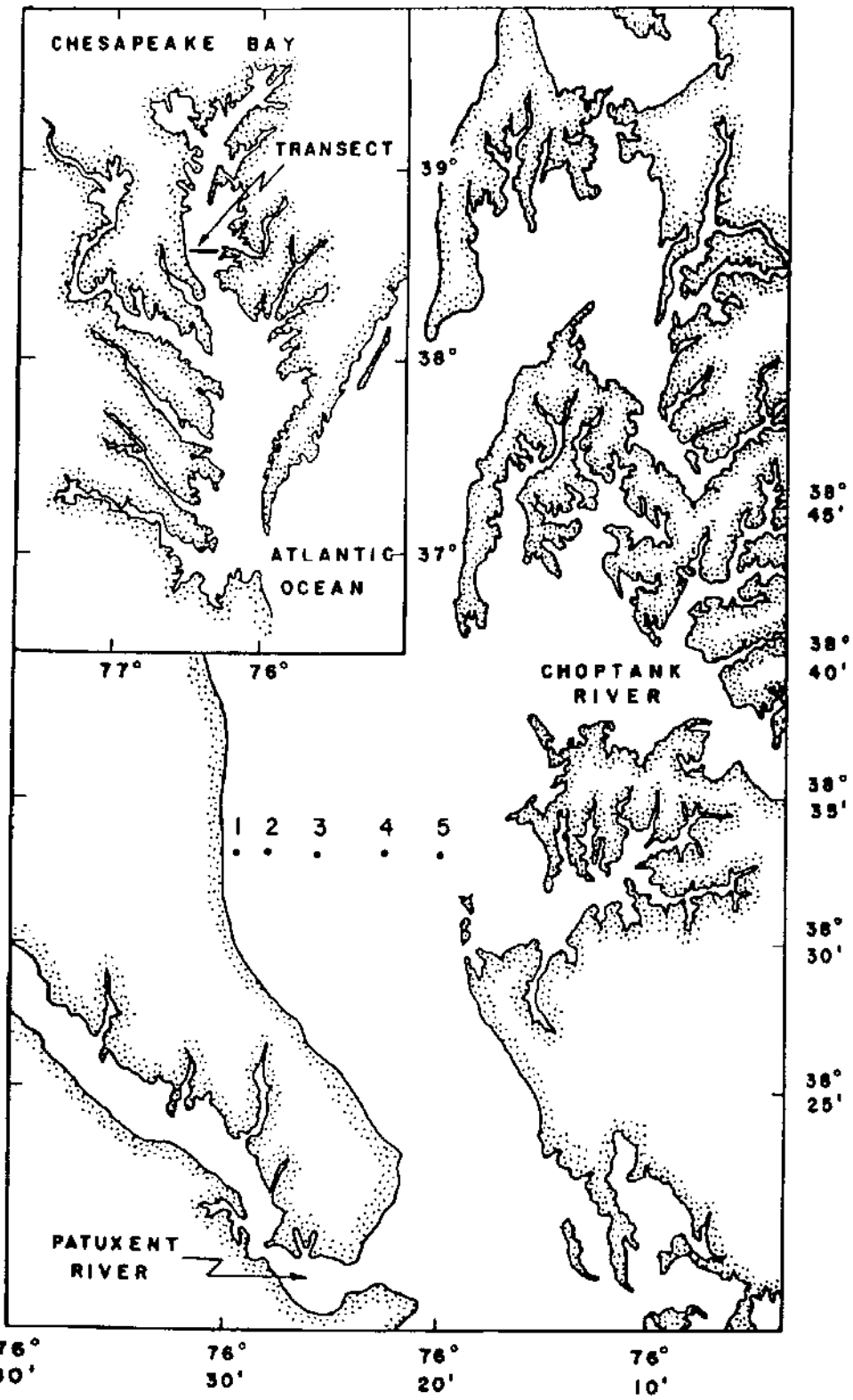
Figure 1. Study area and the location of the CHOP-PAX transect.

BOTTOM LAYER OXYGEN
Station 03
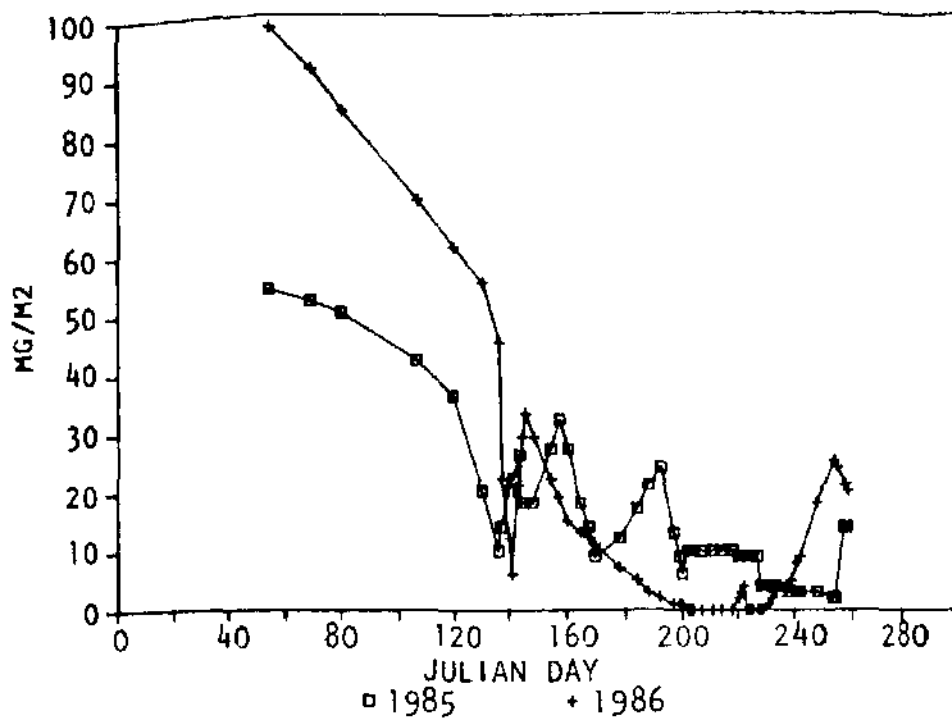
Figure 2. Dissolved oxygen concentrations below the pycnocline in 1985 and 1986.

WATER COLUMN CHLOROPHYLL
Transect Mean
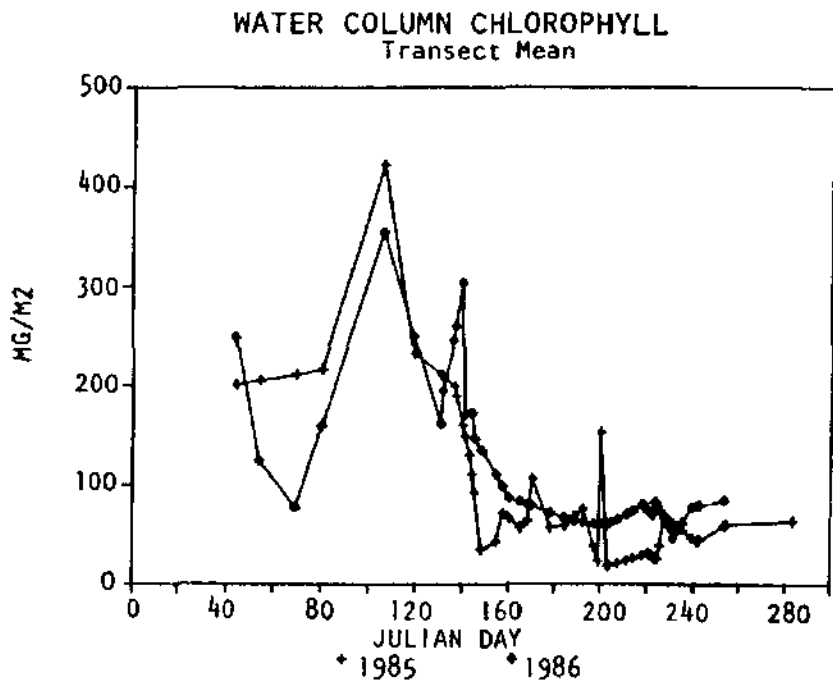
Figure 3a. Water column chlorophyll a concentration in 1985 and 1986.

PRODUCTIVITY/CHLOROPHYLL
Transect Mean
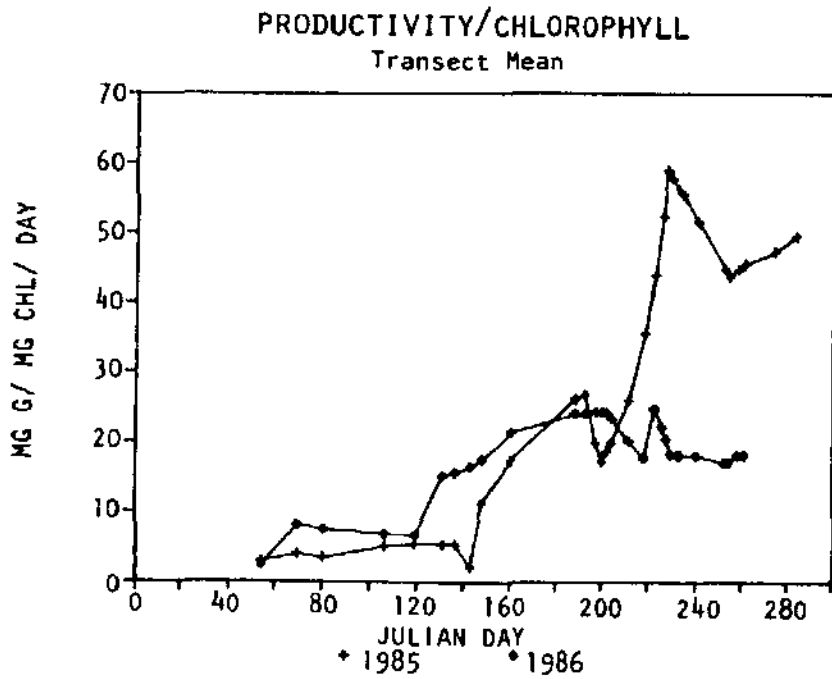
Figure 3b. Chlorophyll-specific phytoplankton production in 1985 and 1986.

CHLOROPHYLL VS. SUSQUEHANNA FLOW
Seasonal Means
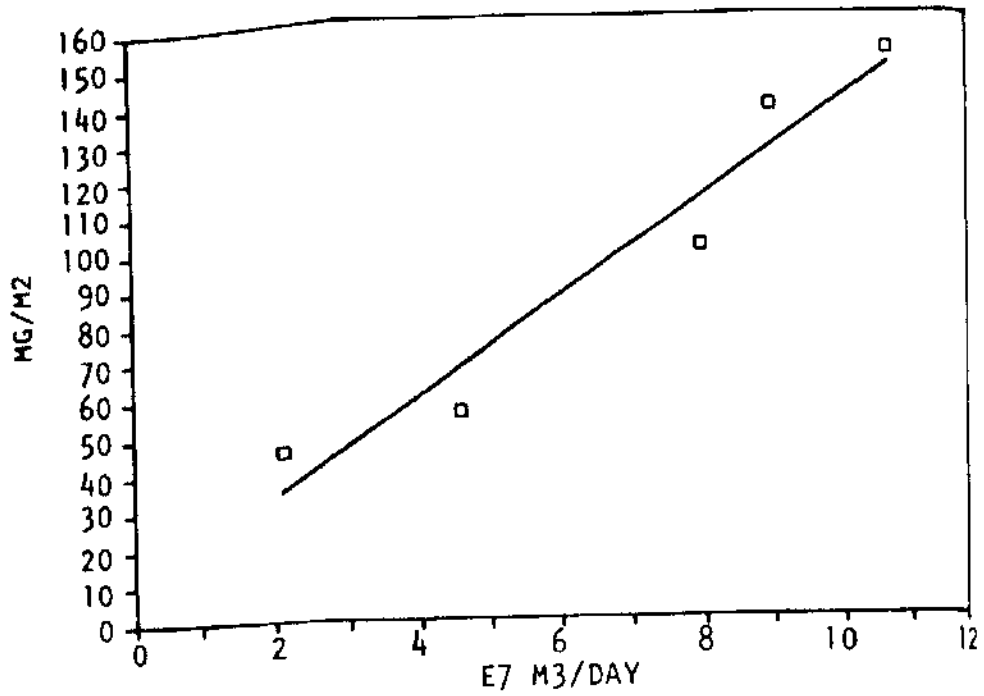
Figure 4. Relationships between seasonally averaged chlorophyll a concentrations and the discharge of the Susquehanna River.

SOURCES OF BIOCHEMICAL OXYGEN DEMAND IN THE CHESAPEAKE BAY: THE ROLE OF MACROPHYTE DETRITUS AND DECOMPOSITION PROCESSES

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The overall objective of this study is to determine the relative contribution of macrophyte detritus decomposition to the depletion of oxygen and the sequestering of nutrients in the lower Chesapeake Bay. Though the decomposition of massive amounts of phytoplankton biomass produced by elevated nutrient levels is believed to be a major cause of anoxic conditions in the Bay, the role of macrophyte litter in the Bay has not yet been adequately evaluated. In addition, the effect of macrophyte litter on excessive anthropogenically-derived nutrients has not been studied. This study will employ a series of field and laboratory experiments to determine:

1. Rate of decomposition of the major types of macrophyte material entering the Bay and the changes in composition during decay.

2. Rate of oxygen consumption of the decaying macrophyte material, the enhancement of this rate by elevated nutrient levels, and the effect of this process on local stable carbon isotope ratios.

3. Composition of the major types of macrophyte material in the lower Chesapeake Bay, and the variation in composition of this material and its resulting detritus between different drainage basins entering the Bay.

4. Contribution of macrophyte-derived material to suspended and sedimentary particulate matter and to the dissolved carbon dioxide in the different drainage basins of the lower Chesapeake Bay by multiple stable isotope analysis.

5. Proportion of oxygen consumption by suspended and sedimentary particulate matter that is attributable to macrophyte derived material.

Methods

During the initial stages of this project we have concentrated our efforts on three sites in the York River estuary having differing salinity and inorganic nutrient levels in order to establish a range of BOD and nutrient values typical for sites with low anthropogenic input. These sites will later be compared to sites characterized by strong anthropogenic inputs or with maximal oceanic influence.

The major emphasis has been on autochthonous material from the dominant seagrass, Zostera marina and salt marsh plant, Spartina alterniflora. Quercus sp., the dominant terrestrial macrophyte in the area, was used during the 1986 experiments as a representative of allochthonous organic material. These three species reflect a range in amount of structural material (e.g., celluloses, hemicelluloses, lignins) and nitrogen concentration.

Plant material was collected as close as possible to the time of natural senescence of the plant and was placed in 1 mm mesh bags of nitex nylon or fiberglass reinforced PVC. Wet/dry weight ratios were estimated according to the procedures of Zieman (1975) to provide levels of starting material without artificially drying the fresh samples. Litter bags were attached to the sediment surface at Mumford Island (strong riverine influence, lowest salinity, high-

est particulates), Allens Island (moderate riverine influence, moderate salinity, moderate particulates), and Guinea Point (weak riverine influence, highest salinity, lowest particulates). Triplicate samples were withdrawn at approximately two week intervals for the first eight weeks, and at four week intervals subsequently. The decomposition studies were initiated in July 1985 (Allen's Island site only), April 1986 and June 1986. A winter decomposition study was started in January 1987.

At sample collection times, the litter bags were retrieved, rinsed with sea water to wash away sediment and extraneous material, and returned to the laboratory where the litter remaining in the bags was sorted and any animals removed. Weighed subsamples were taken for BOD determinations, nutrient flux measurements, microbial abundance and bacterial productivity. After aliquots for other analyses were removed, the plant material was weighed, acid-washed in 10% HCl to remove carbonates, and lyophilized. Weighed subsamples of the freeze-dried material were analyzed for carbon and nitrogen content and ash-free dry weight. Subsamples were also removed for analysis of crude protein, crude soluble carbohydrates, crude fiber, amino acid composition, and stable isotope ratios of carbon, nitrogen and sulfur (analysis in progress).

To determine the rates of oxygen consumption of decomposing macrophytes, subsamples for BOD analysis were removed and placed in bottles containing aerated filtered seawater. Initial and final dissolved oxygen levels were determined after 6 hours of incubation in flowing seawater at ambient temperatures. Dissolved oxygen levels were measured using an Orbisphere oxygen probe/meter system.

The effects of decomposing macrophytes on pools of dissolved nutrients were assessed by placing a subsample of decomposed plant material in bottles containing either (a) filtered water from the site, or (b) filtered water to which ammonia and phosphate were added. Initial and final nutrient concentrations were measured in each bottle and rates of nutrient uptake and release determined. Nutrient

analyses were done according to the methods of Grasshof et al. (1983).

Bacterial abundance was determined using the acridine orange direct count technique and bacterial productivity measured using ^{3}H-thymidine incorporation into bacterial DNA. The abundance of fungal hyphae was estimated using the Jones-Mollison agar-film technique.

Results

Estimates of Decay Rates

The rate and the extent of dry weight loss was similar for Spartina and Zostera. The carbon/nitrogen ratio decreased in Spartina litter but changed little in Zostera. Changes in the total microbial (bacteria + fungi) and bacterial biomass were consistent with dry weight loss and C/N ratios. The total microbial biomass associated with the detritus never exceeded 1% of the total detrital mass. The ratio of bacterial to fungal biomass ranged from 1:1 to 51:1. Early increases in bacterial productivity with Zostera and Spartina litter were coincident with the period of rapid weight loss, presumably as a result of leaching of soluble plant materials. Subsequent rates of productivity were lower, reflecting bacterial utilization of the remaining particulate material rather than readily leached soluble materials. Growth rates and rates of carbon incorporation were highly variable throughout the course of decomposition.

Nutrient Fluxes

The potential for Spartina, Quercus and Zostera litter to sequester or release ammonium and phosphate from or to the water column was measured at ambient and enriched concentrations of nitrogen and phosphorus. In the samples analyzed to date, no apparent differences were observed among sites or plants. Decomposing macrophyte litter released ammonium to the water column at both the ambient and enriched concentrations while phosphate was either removed or unchanged.

Oxygen Consumption

No differences in oxygen consumption were detected among the sites for any plant material. However, Zostera litter exhibited a greater biological oxygen demand at all three sites than either Spartina or Quercus, which showed similar patterns of oxygen consumption.

Remaining Project Activities

In 1987 sampling and decomposition experiments will be conducted in the James River, a river with a strong anthropogenic input, and on Virginia's eastern shore, an area with maximal oceanic influence and minimal human impact. These sampling stations will be located at established Bay research stations where physical and chemical water quality measurements are taken at regular intervals so that seasonal interactions of temperature, salinity, dissolved nutrients and oxygen, and particulate concentration on decomposition can be examined.

Based on the results of these studies, a predictive model will be developed that will be used to estimate the influence of macrophyte derived carbon on the carbon budget of the lower Chesapeake Bay, and the contribution of this carbon to the anoxia problem existing in the Bay.

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DISCUSSION

Mountford: My feeling is that oak leaves tend to be very refractory and that some of that material might reside from year to year on the bottom. Is that consistent with your findings?

Blum: Yes, oak leaves retain their integrity for a much longer period; Spartina and Zostera decay at a much faster rate than Quercus. I think what might determine how long material hangs around is how much physical action the leaves are exposed to -- how much grinding up into small particles.

Garber: Do you suspect that the decay of macrophyte detritus might make a significant contribution to the setup and maintenance of anoxia/hypoxia in the Bay? If you do a back-of-the-envelope calculation -- if you took all of the macrophyte material and dumped it into the Bay in the deep channel and rot it there, would you see the signal?

Blum: That's difficult to answer, because at this time we don't have an idea on how much macrophyte material there is in the Bay. We need better estimates on how much is really there. But in localized areas where there are extensive grass beds, it could be significant, or where you have a Spartina marsh with material washing in.

Garber: My reason for asking is that Chesapeake Bay is generally characterized as a plankton-based system.

Blum: Right, and we don't dispute that at all. We believe that it is phytoplankton-based, but we want to know what contribution the macrophytes make. One of the most important things is what happens to the nutrients and the nutrient cycling during macrophyte decomposition. For example, phosphate uptake, possible nutrient limitations, and so forth.

Mills: I would like to speculate on that — if the data show something different in the next year, then I will come back and tell you something just the opposite -- but I think that Linda's correct that macrophyte detritus can be extremely important in localized areas. If it is being trapped in some spot, you can soak up tremendous amounts of oxygen — very large oxygen demands are associated with that decaying material. For the whole Bay, looking at the numbers we saw this morning, I am not convinced now it makes a significant quantitative contribution to the overall oxygen depletion problem.

Garber: I think also from our historical perspective the contribution is an interesting one -- if you look at the history of SAVs in the Bay, the area which they cover fluctuates violently, from very large to almost infinitesimally small, so whether that contribution is significant depends on looking at some of these historical trends.

Mills: The only problem with the calculation you want us to make is the distributional pattern. Some areas are readily scoured (with no detrital buildup), and in some areas there are pretty thick mats -- so we are going to have to get some idea of the actual distribution of the material as it sits on the sediment surface.

Question: Are there any time periods when the detritus is released?

Blum: There are two time periods: Zostera shows a biannual cycle, it will be senescing soon and will be senescing again in the fall. Spartina of course senesces in the fall and washes off the marshes in spring.

Mountford: (To Malone) Your data shows this late spring phytoplankton "check" in both of the years — I notice in Larry Haas' data that in his DO scatter plots (temperature vs DO), the lows show a bimodality around 23C. I wonder if those two are related, the reduction in phytoplankton "rain" into deeper water and a subsequent reduction in oxygen demand in the water column?

Malone: What we have seen consistently between years and between stations is that the crash in phytoplankton always occurs at around the same time and always when DO gets low. Though the effects of low dissolved oxygen on algal mortality in the dark are not known -- virtually nothing has been done -- I think a good case could be make that they don't survive very well, and there is probably a very rapid mortality.

Tuttle: Could I add something to that? In 1985, before the phytoplankton crash, there was a bacterial crash, which is the opposite of what you might expect -- the other point is that the phytoplankton crash was accompanied by a decrease in water column BOD, too.

Jonas: Drops to less than half of what it was earlier.

Question: You have turnover rates for orthophosphorus and ammonium, and made some speculation on nutrient limitation from them. Do you have anything for nitrite or nitrate, and wouldn't that be important also in terms of the potential for limitation?

Fisher: I didn't measure anything with nitrate with the set of data I showed here -- there are other data that I have on nitrate uptake in the Bay, but very few observations on nitrification in the water column. I think Jim McCarthy has done some work on the rates of nitrification in the water column. But in terms of nitrogen limitation, ammonium is the preferred form for phytoplankton -- nitrate is consumed, but if you are going to look at limitation and the processes, the main source of nitrate is river inflow on an annual basis, I think. The main source of ammonium is in situ recycling -- a minor contribution from rain or terrestrial inputs. If you look at the two on an annual basis, the total amount of ammonium made available via recycling processes is far in excess of the amount of nitrate introduced via river input.

Kemp: But, then again, at levels where ammonium is limiting, previous studies have shown that phytoplankton will switch to nitrate if it's available.

Comment: New nitrogen is ultimately going to be added to that ammonia flux -- the nitrate gets taken up by the phytoplankton and it ultimately enters the ammonia flux -- does all the nitrate coming in end up increasing the ammonium flux?

Fisher: That's right -- virtually all the nitrate coming into Chesapeake Bay is consumed -- either directly by phytoplankton or denitrified in sediments. Virtually none of the nitrate escapes out onto the shelf.

Haas: So the question is, is it better to keep it cycling around in the ammonia pool rather than settling out? Is that the control that needs to be made?

Answer: That is one way to look at it, but it may not be amenable to management.

Haas: It may be amenable in a sense that we talk about nutrient inputs changing rates of production. Again I go back to the idea that nutrient inputs may change species composition. And if your species are small cyanobacteria or flagellates that are being recycled in the microbial food web, versus diatoms. . . .

Going back to your differences in standing stock in '84 and '85 -- why there was more in one year than another? If it's a grazing factor, if the grazing is different between years it may be because species available for grazing are different. This goes back to those ideas of nutrient inputs changing species composition, which could be just as important as changes in rates of productivity.

Fisher: But those changes could also be due to things such as temperature, salinity, depths of mixing which can influence species composition, and so forth.

Haas: True, there are many other factors besides nutrients that could do it.

Mountford: I want to ask you about the situation in the 17th century -- presumably right now we are sort of trying

to "starve out" phytoplankton in Chesapeake Bay in order to improve conditions. Would your nitrogen and phosphorus recycle rates have been extremely high under oligothrophic conditions in the 17th century? What does that mean for the species composition Larry was talking about?

Fisher: Well, that is sort of like doing an evolutionary experiment -- is that what you are asking? If you look at a trophic gradient -- when you go offshore from a shelf situation to blue water, which is essentially what you're trying to do in time here -- the evidence is that nitrogen standing crops decrease and turnover rates increase as you move from eutrophic to oligotrophic, so presumably what was happening in the 17th century was that you had lower inputs, lower standing crops and more intensive recycling of that material than occurs now.

Mountford: So the recycling rate may be an "emergent property" of the phytoplankton community that we may want to keep an eye on -- maybe even manage for direction -- or is that too much?

Fisher: Not sure I want to answer that one!

D'Elia: The important thing to make clear here is the difference between new production and production driven by nutrient regeneration. Ultimately, in the links to hypoxia, new production is of concern -- something that results in the accumulation of organic matter which can be moved some place and be concentrated, decay, and use oxygen. Recycling can occur without any net change whatever in surface waters -- oxygen will stay exactly the same and the system can spin as fast as it can without any effect on hypoxia when consumption proceeds apace with production.

Mountford: But recycling rates go down as new production goes up?

Fisher: In relative terms, yes, but in actual terms it may not. Chris and I were discussing this earlier -- the point I want to make is not that you consider recycling in terms of oxygen problems in the Bay -- recycling terms per se are not

what drives hypoxia. It is the inputs getting into the surface layer, either from above, laterally, or from below the pycnocline, because that's what drives the production of organic material in surface waters and the amount of particles dropping back across the pycnocline. If you look in the context of total supply, the recycling in the water column is really a very important process. Some of the organic material which crosses the pycnocline is degraded in the water as well as in the sediments and then comes back up again [as nutrients]. You have to think of recycling in terms of all the processes which make N and P available for phytoplankton. I would just like to add that Jay Taft did estimates of N and P regeneration in the water column based on oxygen respiration rates. He applied an R/Q ratio and Redfield Stoichiometry and computed P values right on top of the numbers I measured directly. His N figures were off by a factor of 2. This actually turned out to be a useful exercise, to take the respiration data and go through all those calculations, as it comes out not very different from the actual measured values. But what they failed to do in that document was to put all that into context of "what are all the processes?" — they only looked at inputs.

D'Elia: You need to look at recycling rates in the water column to understand what happens to particulate fractions; differential rates of N and P cycling can do a lot to partition out nutrients and ultimately affect the fate of allochthonous nutrient inputs.

Newell: From a zoologist's point of view, I calculated that prior to the major harvest of oysters in about 1880, there were enough oysters in the Chesapeake Bay to cycle the entire volume of the Chesapeake Bay once every six days. The current existing oyster population can only do this once every 180 days. This suggests that oysters were very important nutrient recycling agents. John Smith reported that he could see the bottom of the Bay when he first explored it in the 17th century. Oysters are also very important for biodeposition and for taking sediments out of suspension. In terms of our over-harvesting a resource, that could also be affecting the environment directly.

D'Elia: I think that is the single most understudied thing that we really need to get a grasp on.

Tuttle: What I think we should do is strongly consider aquaculture -- on rafts; it won't do any good to put them on the bottom these days, but we may be able to affect things by putting them on top for awhile. I don't think it is as "off the ceiling" as it may sound.

Jonas: What you're doing by putting oysters on rafts is getting particulate matter to the bottom a lot faster -- how that is going to impact DO is another question.

Newell: Of course the oysters are taking out some nutrients for their own growth, so if you are harvesting them you're taking out nutrients.

Question: Tom, given the link you have mentioned between respiration and nutrient recycling, do you have information on nutrient recycling in the water column below the pycnocline and for sediment regeneration to make a "guesstimate" of the relative contribution of water column vs. sediments to oxygen demand?

Fisher: The data that are available could be used to estimate ammonimun and phosphate production per square meter in the water column below the pycnocline and compare that with what's happening in the sediments. The problem is the limited number of samples: can you let one sample represent the whole pycnocline? There may be local structure and hot spots that you don't see. . . but you can make an order of magnitude estimate of that, although I haven't done it yet.

Boynton: There were some differences in anoxia between the various years studied. But looking at it the other way, the differences between years are pretty trivial. Every year oxygen decreases a lot; some years actually gets to zero -- true chemical zero. In most years it becomes highly hypoxic in any case. Given the amount of oyxgen you have to take out of the water to get it to hypoxic conditions, isn't it reasonable to assume that, in terms of the amount of bio-

logical material available to create anoxia, we're saturated. The real question is: why is there any oxygen down there? If we have biological saturation in terms of oxygen-consuming capabilities, then the explanation for why we have any variation from year to year has to "revolve around" the physics. I hate to say this, I really do, but that's the factor -- there may be some subtle features which we are not used to looking for that are key factors in generating this year-to-year variability.

Boicourt: If we are going to distinguish the effects of man, an important taxpayer question in terms of nutrient controls, we have to know the answer to that question very carefully, well enough to predict year-to-year variation. It's nice that we do have this variation as a signal to help us track things down. We know there are lots of physical processes to get oxygen down there, and we know there's consumption, the question is -- what's the dynamic balance? We could essentially "get the physics out" so the biologists could then come in and work out the rates and processes and thereby determine the effect of nutrients on the system. I think that we're a lot closer to doing that physically than we were even a few years ago. A simple model like I showed this morning could be cranked out on the computer and could separate out the rates measured as a first-order estimate.

Comment: If we're trying to monitor the response of the system to controls, maybe we shouldn't be measuring DO, since that is the interplay between the physical factors and the consumptive factors. Maybe we should just worry about those sources we can control, such as oxygen demand -- we could just measure water column oxygen demand, sediment oxygen demand as indicators of whether we're making progress. The measuring of DO is just a confounding factor in this whole sorting out of the physical versus the anthropogenic factors.

Jonas: In a minute I'll put up some data showing respiration rates measured against some of these parameters and bacterial biomass in particular; the correlations are quite striking. Hugh Ducklow brought it up earlier -- this is one

variable that hasn't been measured in the past, partly for technical reasons, partly because it's very manpower-intensive to do, but the relation to oxygen consumption is there.

Kemp: Probably the most provocative thing we've seen all day is Tom Malone's five-point regression between riverflow and chlorophyll concentrations. I really like it because it's consistent with something Boynton and I have been saying before but. . . while it's a nice story, is it real?

Malone: At least over that segment of the Bay, there are generally more nutrients in terms of phosphorus and nitrogen than you would expect to have any effect, at least on growth rate. Now the yield question is another story; and our data suggest that there is some relation between nutrient input and yield, which would hark back to the new nutrients/new production issue. But there is no obvious relationship between the nutrients and any of the biological parameters that were measured. When you see variations in physical fields that you would expect to affect nutrient flux, you see a phytoplankton response or a bacterial response or whatever, but there is no experimental basis for expecting that relationship. Scott Nixon sees a similar relationship in the MERL mesocosms. Those were seasonally averaged figures -- freshwater input and chlorophyll concentrations which were used in the regression.

CHESAPEAKE BAY DISSOLVED OXYGEN DYNAMICS: ROLES OF PHYTOPLANKTON AND MICROHETEROTROPHS

Robert B. Jonas
George Mason University

Objectives

The overall objective of this work was to describe the microbiological, both autotrophic and heterotrophic, nutrient and physical hydrodynamic relationships over seasonal cycles with sufficient resolution in time and space to determine the conditions influencing oxygen depletion across the affected area of the Chesapeake Bay. To attain this goal we are conducting a field investigation with the following objectives:

1. Assess the importance of phytoplankton production as a source of organic matter to bottom water.

2. Evaluate the significance of phytoplankton production over the shallow flanks of the main channel relative to production in the channel itself as a source of organic matter.

3. Determine the importance of heterotrophic microorganisms in the water column and their associated metabolic processes as consumers of organic matter and dissolved oxygen, and establish how the microheterotroph community varies in relation to phytoplankton production, organic inputs, biochemical oxygen demand (BOD) and dissolved oxygen concentrations.

4. Establish how variations in vertical water column stratification over seasonal cycles influence these relationships.

5. Identify the southern boundary of the oxygen-depleted zone.

A sizeable data base has been developed for the upper, mesohaline portion of the Bay through cooperative research efforts funded by the Maryland Sea Grant Program, the Environmental Protection Agency, George Mason University and the University of Maryland. No like data were previously available from that portion of the Bay south of the Potomac River. Therefore, we concentrated our investigation on the processes occurring in the Virginia portion of the (lower) Bay. The objectives of this focused effort are twofold:

1. Establish the interannual variability in the processes driving oxygen depletion in the lower Bay,

2. Determine if there are major differences in the trophic dynamics driving the process of oxygen depletion in the upper and lower Bay by developing a data base sufficient for comparison to that which has been, and is currently being developed for the Maryland (upper) mesohaline portion of the Bay.

Progress

During 1986 we completed 15 cruises, between February and December, in which we occupied stations along 4 transects arrayed across the main axis of the Chesapeake Bay. Transects are located at the Chesapeake Bay bridge, between Dares Beach and the Choptank River, at the mouth of the Patuxent River, and off the mouth of the Great Wicomico River, south of the Potomac River. In addition we participated in two 30-hour anchor stations in May, and one in August 1986 along the Dares Beach/Choptank River transect. During most of the 1986 cruises we occupied at least 18 stations and collected samples for the entire suite of parameters described in the original proposal.

Vertical profiles of temperature, salinity, dissolved oxygen, chlorophyll a, and bacterial abundance were made at each station. Phytoplankton production, bacterial pro-

duction, bacterial metabolism of amino acids (phytoplankton protein hydrolysate) and glucose, water column oxygen consumption and biochemical oxygen demand were also estimated, along with dissolved inorganic nutrients (phosphate, nitrate, nitrite, ammonium and silicate), particulate organic carbon and nitrogen, and phytoplankton species composition were also measured at these stations.

Preliminary Results

Taking the goals of this investigation into account, this description of results will concentrate on a comparison of heterotrophic processes in the waters along the southernmost transect (lower) with those in the more northerly regions.

With regard to dissolved oxygen (DO) levels, anoxic conditions developed in the upper mesohaline portion of the Bay by the third week of June 1986. By the first week of July, hydrogen sulfide was detected in upper Bay deep water. Anoxic conditions spread south during July, reaching the area off Point-No-Point (north of the Potomac) by July 22. By August 7 anoxic conditions existed from the Annapolis Bay Bridge to below the Great Wicomico River. Along the southernmost transect anoxic conditions existed from the mainstem channel toward the west at depths greater than 7 m. The upper boundary of the anoxic zone was shallower at the southern transect (7 m) than at the Bay Bridge (12 m). The anoxic zone was closely associated with the intense salinity gradient which existed during 1986. At the southern transect, water to the east of the mainstem channel which was weakly stratified remained oxygenated throughout the season. We confirmed the occurrence of midwater minima in oxygen concentration and even midwater anoxia at several of the main axis deep stations. This may suggest that water column oxygen consumption associated with recent organic carbon inputs, which could accumulate at the pycnocline, is a significant factor driving oxygen depletion.

As in 1985, the Chesapeake Bay streamflow was markedly below average in 1986. However, indications are that,

because of early spring runoff, the water column remained strongly stratified during that summer. During late August a series of storms passed over the Bay area. The strength of salinity stratification was reduced and bottom water throughout the Bay was reoxygenated.

With regard to heterotrophic parameters specifically, we had previously shown that the Chesapeake Bay supports an unprecedentedly high bacterial biomass (>10 million cells per ml) during the late summer. During 1986, bacterial abundances throughout the Bay rose from about 0.9-2 x 10 cells/ml in late winter to more than 10 x 10^6 cells/ml by mid-May. Bacterial abundances in the water above the pycnocline exceeded the 10 million per ml level first in the upper Bay and then in the lower Bay about a month later. By early August bacterial abundances greater than 20 x 10^6 cells/ml were common throughout the entire research area (Bay Bridge, 38 x 10^6; Great Wicomico River, 27 x 10^6 cells/ml). Abundances declined throughout the late summer and fall, reaching 1-2 x 10^6 cells/ml throughout the mid-Bay by December.

High levels of bacterial production (estimated from thymidine incorporation - TdR) and metabolic activity (amino acid - AATR and glucose - GLTR turnover rates) were associated with increases in bacterial abundance. By mid-May glucose turnover rates in the upper Bay exceeded 20%/h and TdR approached 150 pmol/l*h (February rates were: GLTR 1-9% h, TdR 8-40 mol/l*h). By early June GLTR greater than 40%/h were observed from the Bay Bridge to the Great Wicomico River especially along the western side of the Bay. At the same time the highest AATR values (10%/h) were observed near the western shore in the lower Bay. TdR continued to increase in the upper levels of the water column during the summer. By late July values of 500 to 800 pmol/l*h, some of the highest values ever recorded for a natural aquatic system, were found both in the northern and southern parts of the research area. TdR values were highest along the western side of the Bay. Interestingly, TdR values in the area off the Patuxent River, in the middle of the study area, were only about 250

pmol/1*h or less. Metabolic rates and production rates remained high throughout August over the entire region. During this period the highest (AATR 45%/h, GLTR 37%/h) metabolic rates occurred along the western side of the southern transect. The heterotrophic processes, utilizing both particulate and dissolved organic matter and driving oxygen depletion, are of a similar order of magnitude throughout the mesohaline portion of Chesapeake Bay during the summer. Bacterial production and metabolic rates declined in early September in the lower Bay and about 2 weeks later in the upper Bay. By December TdR was less than 20 pmol/1*hr and GLTR and AATR were 1%/h or less.

There are a number of trends which appear to be consistent with regard to these parameters. High rates of heterotrophic activity develop first in the northern Bay and later in the southern Bay. The highest rates are consistently found along the western side of the Bay. Under summer conditions very high rates of heterotrophic activity and bacterial abundances occur throughout the area of the Bay affected by anoxic and hypoxic conditions. Under the highly stratified summer conditions mid-water maxima for microbial heterotrophic activity and bacterial production often occur in association with the pycnocline. A higher resolution depth profile of these parameters is needed to establish the importance of this phenomenon with regard to integrated water column oxygen consumption.

In terms of organic inputs to the system we measured biochemical oxygen demand (BOD) in the Bay. This parameter provides a very useful estimate of the amount of easily metabolizable organic carbon available to support heterotrophic metabolism and to drive oxygen consumption. Over the entire year BOD levels ranged from about 0.5-7.5 mg/1 in the surface waters. During February BOD in the surface waters of the lower Bay (3.8 mg/1) was more than twice that in the upper Bay (1.4 mg/1), although there appears to have been an accumulation of BOD at the pycnocline in the upper Bay. Mid-water maxima of BOD were common during the spring but not during the summer. Throughout the highly stratified portion of 1986 (June-August), BOD rapidly declined with depth. We speculate

that the high rates of bacterial metabolism rapidly utilize this organic matter especially in the pycnocline region. In late spring BOD levels in the northern Bay (3 mg/l) generally exceeded those in the southern area (1 mg/l). Near the Bay Bridge surface BOD levels were commonly greater than 3 mg/l and occasionally reached 5-7 mg/l. During midsummer, however, highest values occurred in the southern Bay especially along the western flank. BOD values exceeded 7 mg/l for a period of several weeks during July/August in the surface waters along the western side of the Great Wicomico River transect.

In the surface waters BOD was mostly particulate and probably consisted primarily of phytoplankton cells. In deeper waters, however, as much as 50-95% of the total BOD was present as "dissolved" (passing a Gelman GF/F glass fiber filter) organic matter.

Because of the extended cruise schedule during 1986, data analysis is still not complete. In-depth comparisons of primary production and heterotrophic processes remain to be completed. We limited this preliminary abstract to the heterotrophic components, while nutrient and phytoplankton dynamics during the 1986 season are presented elsewhere.

BACTERIAL CARBON POOLS AND FLUXES IN CHESAPEAKE BAY PLANKTON

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We have been investigating the distribution of bacterial abundance and production in the water column of the mid-Bay region since summer 1984. The principal emphasis of our work has changed somewhat each year, but taking the three years together, a large data set has been obtained and some generalizations about the importance of bacteria in the plankton system of the mid-Bay can be made. In this abstract we will summarize some of our findings, point out their relevance to the anoxia problem, and outline directions for future research. Most of the discussion which follows is derived from analyses of the 1984-85 data sets. The conclusions reported here are preliminary.

Our data set is based on measurements of bacterial abundance via acridine orange direct counts made on an epifluorescence microscope, and of bacterial production via incorporation of tritiated thymidine into TCA-insoluble cell fractions. These are the most widely recognized and utilized methods available for measuring these parameters. For the data reported here, we assume that each bacterial cell has 20 fg of carbon, and that 2×10^{18} cells are produced for each mole of thymidine incorporated. There is much support in the literature for these values, but it is important to our conclusions to note that in this case these assumptions lead to conservative estimates of bacterial biomass and production.

Our sampling has shown that bacterial abundance is low in the winter and early spring (ca. 1-3 million cells/ml) then

rises to a peak in late summer. Upwards of 20 million cells/ml are occasionally observed on the flanks of the mid-Bay in June-September. In our combined 1984-85 data sets (n=1200 samples), about half the abundance values are greater than 7 million cells/ml. This is notable because values of 5-7 million cells/ml are generally the highest values reported in other well-sampled estuaries (e.g., Wright and Coffin, 1983). Patterns of thymidine incorporation are similar. Both abundance and thymidine incorporation are slightly higher near the Bay Bridge than further south, higher on the flanks than in the mid-channel, and higher in the surface layer than in the bottom, especially under stratified conditions when there is low oxygen in the bottom layer. In general, the temporal and spatial patterns correspond to those for phytoplankton biomass and production, suggesting that bacterial metabolism is supported by the products of in situ phytoplankton production during the same year. These findings are described in greater detail in Malone et al. (1986) and in our reports to the EPA Chesapeake Bay Program.

Comparison of the bacterial and phytoplankton data sets shows that from late spring through the summer, bacterial biomass and production are very high throughout the region from the Bay Bridge to the Potomac, i.e., the region impacted by anoxia. Using the conversion factors mentioned above, and assuming a carbon:chlorophyll ratio of 50, we estimate that bacterial biomass and production are about equal to phytoplankton values in many samples. In our 1984 data set (n=400), bacterial biomass is greater than phytoplankton biomass by up to a factor of 3 in about half the samples. This means that the bacteria are a highly significant pool of carbon in the Chesapeake Bay plankton. In the mid-Bay region, more carbon appears to be flowing from phytoplankton to bacteria than in other estuaries, and this is unequivocally true in comparison to the ocean.

This conclusion is supported by the data on production rates. Most studies in the literature show that in lakes, estuaries, and in the coastal and open sea, bacterial production is about 5-30% of daily primary production (Ducklow, 1983). It is generally supposed that bacteria have

conversion efficiencies of around 50%, suggesting that about 10-60% of the total primary production eventually flows through the bacteria. In this regard, the situation in Chesapeake Bay, now supported by a large body of data, is somewhat extreme. In our combined 1984-86 data sets, bacterial production in the euphotic zone alone averages about 150% of primary production. This is hard to explain even if bacteria are highly efficient, unless they depend to a great extent on allochthonous carbon. Yet several lines of reasoning lead us to believe that this is not the case. First, as we mentioned above, bacterial variability corresponds in general to phytoplankton patterns. Furthermore it is well-established that most of the particulate organic carbon in the mid and lower Bay is derived from in situ production. We also know that the dissolved compounds used by planktonic bacteria have turnover times of a few hours at most. These considerations make it seem unlikely that bacteria are supported largely by remote sources of organic matter. This leaves three alternatives: (1) our measurements are wrong and our assumptions are incorrect, (2) high bacterial production is a consequence of accomposition of accumulated phytoplankton biomass on scales of weeks to months in late spring or, (3) the plankton system in Chesapeake Bay has been modified in such a way that a very large amount of primary production is cycled through the bacteria by mechanisms we do not yet understand.

Without going into much detail here, we will state (not too surprisingly) that we lean toward the latter explanations, while leaving open the possibility that our data may require reinterpretation as more data come in. However, we note again that we have used conservative assumptions in converting our data to carbon units. Even using the most conservative factors, we estimate that on the average 70% of the primary production is metabolized by bacteria on a daily basis.

In 1986 we began to analyze experimentally the assumptions we have used for making our estimates of bacterial production. For example we have been making independent measurements of bacterial growth rates in low and high levels of oxygen. In general the preliminary findings

support the idea that bacterial production is very high. We have also begun to investigate the effect of anoxia on the incorporation of thymidine into DNA, RNA and protein in bacterial cells. Our findings show that in low oxygen conditions, substantially less thymidine is incorporated into DNA, compared to samples with saturated oxygen. This means that great care must be taken when interpreting thymidine data from the bottom layer in summer. Our estimates of bottom layer bacterial production in summer take this effect into account, and show that in July-September, bacterial production is only about 5-20% of the overlying primary production. We conclude that hypoxia and anoxia have a profound effect on bacterial metabolism, and thus probably on the patterns of carbon flux in the plankton, which are otherwise bacteria-dominated.

What is the importance of these data for understanding anoxia? We have shown that the Chesapeake Bay appears to be notable in that a very large amount of carbon is diverted through the bacteria, and that bacteria are one of the largest single pools of biomass in the plankton. Estimates of biomass-specific oxygen utilization rates vary widely, but even the lower ones, when combined with our data, show that most of the measured water column oxygen demand could be met by bacteria alone.

We are not yet sure of the validity of our estimates of bacterial carbon flux, except to say with certainty that they are as high or higher than in most other systems studied to date. Similarly, we do not understand the processes supporting this very high bacterial production. But we can state safely that understanding the processes generating and maintaining anoxia in Chesapeake Bay requires continued research on water column processes in general and bacterial processes in particular.

During the next year or two, we plan to fill in poorly sampled times of the year and to investigate in greater detail the factors influencing our assumptions about bacterial carbon fluxes, including the effects of lowered oxygen on bacterial physiology. We also plan to try some modelling approaches to see if they shed light on the ecological mechanisms capable of supporting large bacterial production.

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IMPLICATIONS OF MICROZOOPLANKTON GRAZING ON CARBON FLUX AND ANOXIA IN CHESAPEAKE BAY

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As part of the NOAA-Maryland and Virginia Sea Grant-EPA sponsored multi-investigator collaborative research program on anoxia in mid-Chesapeake Bay in 1986, we initiated a program to determine the role of rapidly growing microzooplankton in grazing phytoplankton and bacteria in mid-Chesapeake Bay. The program was designed around several assumptions: (1) after stratification, cross-Bay "tilting" of the pycnocline causes upwelling of nutrient-rich, low oxygen waters at one side of the Bay which results in high phytoplankton biomass and/or productivity in these shallow areas; (2) phytoplankton response is relatively rapid, theoretically favoring microheterotrophs that could rapidly utilize the rapidly growing autotrophic assemblages; and (3) phytoplankton not grazed might sink to sub-pycnocline microaerobic or anoxic waters perpetuating continued oxygen demand and anoxia in mid-channel waters.

In May, after stratification, but prior to development of anoxic conditions, cross-bay transects were made from $38°23'$ to $38°58'N$. Temperature, salinity and density as well as in vivo fluorescence and dissolved oxygen levels were determined throughout the water column in 3-5 stations/transect. There was little evidence of any cross-bay tilt in the pycnocline and concentrations of chlorophyll in surface waters were low (5.4-9.7 µg/l) and similar from east-to-west at a given latitude. Chlorophyll concentrations did increase with depth and up-Bay, however, primarily due to

high concentrations of the dinoflagellate Prorocentrum and the centric diatom Cyclotella. Sub-surface chlorophyll maxima were observed at and below the pycnocline and can be attributed to up-Bay transport of Prorocentrum.

Since the May cruises did not coincide with any cross-bay tilt of the pycnocline, microzooplankton grazing experiments were conducted with plankton assemblages associated with the sub-surface chlorophyll maxima ("seed" populations for surface blooms accompanying tilting) and, as a contrast, chlorophyll-poorer waters from mid-channel areas (plankton associated with non-tilting conditions).

Individual microzooplankton species were isolated and transferred to tubes containing whole water from the collection depth. Using single or dual label radioisotope techniques, microzooplankton grazing rates (μl/individual/h) on autotrophs and bacteria were determined. Microzooplankton carbon demand was estimated for each species from the product of grazing rate and the available phytoplankton or bacterial carbon. Total carbon demand for the microzooplankton community was estimated from the rates measured in the study and microzooplankton densities. Finally, the quantity of carbon remaining after microzooplankton grazing was estimated from the difference between phytoplankton biomass and microzooplankton requirements.

Phytoplankton distributions in the Bay in May generally reflected the contributions of Prorocentrum and Cyclotella. Phytoplankton carbon ranged from approximately 625-1801 μg/l in the samples employed in the grazing experiments, with total cell densities from 7-15.2 x 10^6/l. Microzooplankton densities ranged from 771-31029 individuals/l. Ciliates were dominant though rotifers, copepod nauplii, and polychaete larvae were also present (note: heterotrophic flagellates were not enumerated).

Large microzooplankton were most numerous at station 858C ($38^\circ 58'$ N) in early and late May, coinciding with highest chlorophyll concentrations (26-28 μg/l) and Prorocentrum densities (6.6 and 6.9 x 10^6/l, respectively); total

microzooplankton densities were 2312 and 4505 individuals/l, respectively. High Prorocentrum densities were associated with high densities of several of the larger taxa, including polychaete larvae and rotifers while the lowest dinoflagellate density $(2.6 \times 10^5$ cells/l) encountered at station 840H $(38^\circ 40'N)$ was associated with the lowest numbers of the largest microzooplankton taxa (<10/l).

In May, microzooplankton grazing experiments were conducted with ten "populations," including rotifers (Synchaeta sp.), polychaete larvae, copepod nauplii, an oligotrich Strombidium and the tintinnid Tintinnopsis acuminata. Grazing rates for taxa feeding on phytoplankton were low, ranging from 0.01 µl/h for T. acuminata to 19.17 µl/h for polychaete larvae. Two Synchaeta species had rates ranging from 0.34-9.74 µl/individual/h. The oligotrich species, Strombidium, was typified by rates from 0.05-1.00 µl/individual/h. Copepod nauplii, at <46/l, cleared 1.44 µl/nauplius/h.

Microzooplankton grazing on bacteria was also low although several taxa had higher grazing rates on the thymidine-labeled particulates. Grazing rates from all experiments ranged from 0.08-3.64 µl/individual/h. The tintinnid T. acuminata, one Synchaeta species and one of two Strombidium populations, was typified by grazing rates of 0.08, 0.53 and 0.38 µl/individual/h, respectively, or rates 8, 1.2 and 8.4 times the grazing rates measured for these species feeding on phytoplankton.

In late August, cross-bay transects at $38^\circ 30'N$ revealed higher chlorophyll (as in vivo fluorescence) in surface waters on the western shore. However, there was little tilt in isopycnals cross-bay and low dissolved oxygen was encountered (at depths >5.5 m) on the western shore only on the 27th. Dinoflagellates, principally Gymnodinium, Ceratium and Polykrikos sp., dominated phytoplankton biomass in samples from the western shore, reaching 1×10^6 cells/l. Dinoflagellate densities in mid-Bay and on the eastern shore were 0.2 and 0.1×10^6 cells/l, respectively. Total microzooplankton densities followed a similar cross-bay trend with

highest densities on the western shore (>9500 individuals/1), dominated by tintinnids (4880-5320/1), oligotrichs (3280-4120/1), "other" ciliates (<480/1) and equal contributions (~194-282/1) of rotifers and copepod nauplii. Microzooplankton densities in stations to the east ranged from 2901-6452 individuals/1 with decreasing contributions for all groups.

Grazing experiments were run with three microzooplankton taxa, the rotifer Synchaeta stylata, a tintinnid ciliate Favella sp. and an oligotrich ciliate Laboea. Experiments were conducted with samples from the western shore and mid-Bay, representing high and low phytoplankton concentrations. The rotifer derived much of its carbon from bacteria. Grazing rates were 4-10 times higher on thymidine-labeled particulate material versus ^{14}C-phytoplankton resulting in bacterial carbon forming 61% and 34% of total carbon ingested. As an herbivore, S. stylata consumed only 0.33 and 0.03 µg C/1/d in the western and mid-channel stations, respectively. Favella sp., recognized as a major predator on dinoflagellates, preferred phytoplankton with grazing rates of 2.06 and 1.77 µl/individual/h, respectively, resulting in the removal of 11.79 and 3.92 µg C/1/day. Bacterial intake, with grazing rates of 0.07-0.09 µl/ind/h, was very low at >0.013 µgC/1/d. Laboea sp. was characterized by the highest grazing rates encountered in the study. The oligotrich grazed phytoplankton and bacteria at 31.16 and 6.30 µl/ind/h, respectively, in the western shore, dinoflagellate-rich station while rates of 2.88 and 3.56 µl/ind/h were obtained in the mid-channel, dinoflagellate-poor station. The rates for the western shore population are somewhat in doubt and thus the lower rates from the mid-channel station were used in all calculations. In mid-Bay, Laboea would remove 12.26 and 0.72 µgC/1/d from the phytoplankton and bacterioplankton, respectively.

Total carbon demand by May and August microzooplankton assemblages was estimated from the products of "average" grazing rates and densities assuming no net growth in either plankton component. In May, microzooplankton herbivory would remove 13-55% of phytoplankton

biomass/d. In August, microzooplankton would consume 21-53% of the available phytoplankton carbon. These data imply that the smallest herbivores in the Bay could be the most important consumer of the phytoplankton.

In 1987, plankton responses to the intrusion of sub-pycnocline water into shallow shoreline areas of the mid-Bay will be examined through a summer field sampling schedule fixed to the local winds. Sample collections along a cross-bay transect at $38^\circ 30'$ N will be undertaken after 4-5 m/sec westerly or southwesterly winds have been observed for 1-2 d. In addition, in order to estimate total daily microzooplankton grazing pressure in a region, grazing and growth rates of the dominant microzooplankton taxa will be determined at several stations.

PHYSICAL AND BIOLOGICAL PROCESSES REGULATING ANOXIA IN CHESAPEAKE BAY: ZOOPLANKTON DYNAMICS

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Zooplankton-Anoxia Interactions

Zooplankton, the dominant herbivore group in Chesapeake Bay, may be adversely affected by anoxic bottom waters because anoxia would limit the normal diel vertical migration behavior of the dominant copepod species; reduce the amount of "available" habitat, thereby increasing competition for food and susceptability to predation; and potentially reduce zooplankton recruitment as a result of copepod eggs sinking into the anoxic bottom waters where they would die.

In addition to being adversely affected by anoxia, zooplankton may contribute both directly and indirectly to the depletion of oxygen in the bottom waters of Chesapeake Bay. It has been observed in other marine habitats that zooplankton aggregate closely above oxygen minimum or anoxic layers. Zooplankton which occur at the oxycline can be over an order of magnitude higher than densities found in other parts of the water column. In Chesapeake Bay during spring, summer and fall when the feeding activity and respiration of zooplankton is highest, aggregations of zooplankton above the oxycline would result in a sink for oxygen. Zooplankton could thus reduce the diffusion of oxygen into the bottom waters thereby contributing to the maintenance of anoxia in the Bay.

Zooplankton may also indirectly contribute to both the initiation and maintenance of anoxia in bottom waters by

their lack, or reduced utilization, of phytoplankton. Un-grazed phytoplankton production would sink to the bottom waters where its decomposition would reduce oxygen concentrations. "Uncoupled" phytoplankton-zooplankton inter-actions would occur when there was a rapid increase in phytoplankton production (perhaps due to an episodic input of nutrients because of wind mixing or pycnocline tilting) which is faster than increases in zooplankton production and grazing; as a result of a bloom of a phytoplankton species that is not eaten by zooplankton such as Phaeocystis sp. or Ceratium sp.; and when zooplankton populations are reduced by predators such as ctenophores. All of these sources of "uncoupling" zooplankton grazing from phytoplankton pro-duction can be important during the period of anoxia in Chesapeake Bay.

Project Description

As a component of the Maryland and Virginia Sea Grant dissolved oxygen program, we are examining the role of zooplankton in the onset and maintenance of anoxia in Chesapeake Bay. Our sampling strategy has been to mea-sure the vertical distribution of zooplankton biomass, abun-dance and grazing on scales of hours-days during seasonal extremes of freshwater flow. To date we have conducted these measurements in May 1986, prior to the onset of anoxia, and in August 1986 when the water column was strongly stratified and the bottom waters anoxic. During the 1987 field program we will measure zooplankton abun-dance and grazing during two-week periods in March, May and August. Additional measurements during the 1987 research program will include estimates of zooplankton nitrogen excretion, in situ oxygen consumption by zoo-plankton and a laboratory study on the effects of anoxia on the hatching success of copepod eggs.

Specific objectives of our research program include:

1. Determining the diel, fine-scale distribution pattern of zooplankton in relation to the density structure of the water column, oxygen concentration and phytoplankton biomass.

2. Measuring the in situ ingestion rate of zooplankton to determine how much of the daily phytoplankton production is grazed by zooplankton.

3. Measuring the in situ oxygen consumption of zooplankton so that their direct contribution to oxygen depletion can be estimated.

4. Measuring the nitrogen excretion rate of various size-groups of zooplankton.

5. Determining the density of gelatinous zooplankton and applying published values of their consumption rates so that we can estimate their role in reducing the phytoplankton-consuming zooplankton (copepods).

6. Examining the effect of oxygen concentration on the hatching success and development times of copepod eggs.

Results to Date

We are currently enumerating the zooplankton samples that were collected during the 1986 field season. The biomass of daytime zooplankton (>64 µm) above and below the pycnocline at the mid-Bay station illustrates the effect of anoxia (Figure 1). In May (Figure 1a), although there was less dissolved oxygen in the bottom water, greater amounts of zooplankton were present below the pycnocline. Zooplankton biomass ranged from 2.8 - 3.2 mg C/m^3 in surface waters and from 3.8 - 8.0 mg C/m^3 in the bottom waters of the mid-Bay station. This pattern of vertical abundance was reversed in August when the bottom waters were anoxic (Figure 1b). On 8/11 when there was a sharp oxycline and no detectable oxygen below 12m, surface zooplankton were over 7 times higher than concentrations found in the bottom water. Over the August study period (8/10-8/27) the dissolved oxygen content of the bottom water of the mid-Bay station increased (likely as a consequence of wind-induced mixing). Thus on 8/20 and 8/27 we observed increasing

concentrations of zooplankton in the bottom water, reaching 47.8 mg C/m^3 on 8/27.

Distribution of copepod nauplii, the dominant food of larval fish, is also influenced by anoxia. Although nauplii densities are lower in May (Figure 2), there are significant quantities below the oxycline relative to abundances in the surface. In contrast, bottom water nauplii densities in August are less than 10% of surface densities until 8/27 when the bottom waters were reoxygenated.

While the grazing rate data from May have been analyzed, we are still processing the August samples. The few grazing samples from August that have been completed indicate that on a weight-specific basis, zooplankton grazing in the surface waters was over twice the values determined from the May cruise (means = 41 ml filtered/mg zooplankton C/h in May; 96 ml filtered/mg zooplankton C/h in August). When multiplied by the biomass of zooplankton in the surface water (means = 3 mg C/m^3 in May, 30 mg C/m^3 in August), we estimate that the grazing pressure by zooplankton in the mixed layer in August is over 20x higher than in May.

Another factor which would indirectly influence how much phytoplankton is consumed is the abundance of predatory zooplankton such as ctenophores and medusae. At five stations across the Bay near the Little Choptank River (5 = eastern, 3 = mid-Bay, 1 = western) the biomass (displacement volume) of gelatinous zooplankton was determined on the May and August time series (Figure 3). In May, the biomass of jellies increased over time and was usually highest off the eastern shore (station 5). In August the biomass of gelatinous zooplankton had increased with the highest mean concentration of jellies off the western shore (station 1). Most of these gelatinous zooplankton at the western shore station were ctenophores in contrast to the eastern stations where sea nettles predominated. As a possible consequence of these distributions, there may have been greater removal of copepods by predation near the western shore, thus releasing the phytoplankton from grazing pressure. If this

postulation proves correct there may be more organic deposition (as phyto-detritus) near the western shore as compared to the eastern Bay.
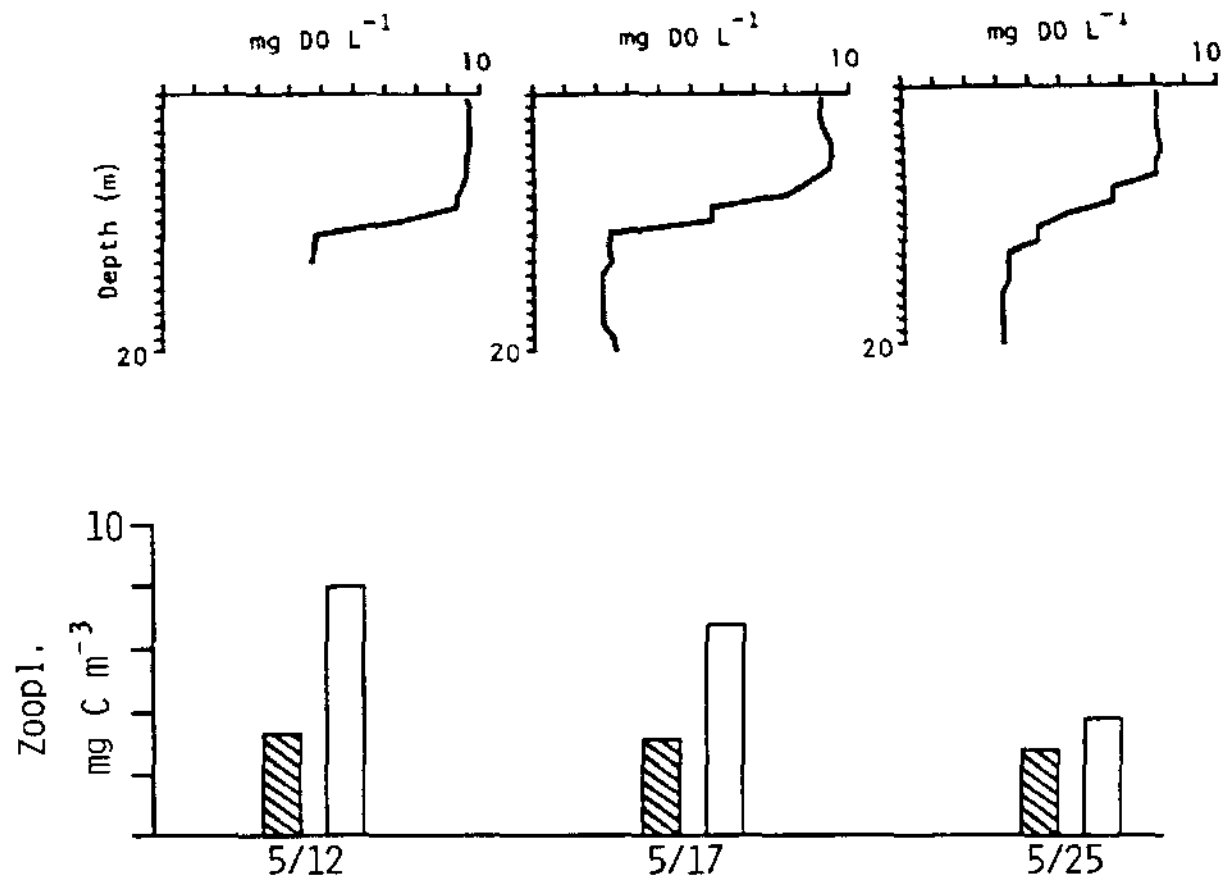
Figure 1a. Dissolved oxygen distribution and zooplankton biomass on May 12, 17 and 25 at a mid-Bay station. Shaded bars are zooplankton biomass above the oxycline, open bars are zooplankton biomass below the oxycline.
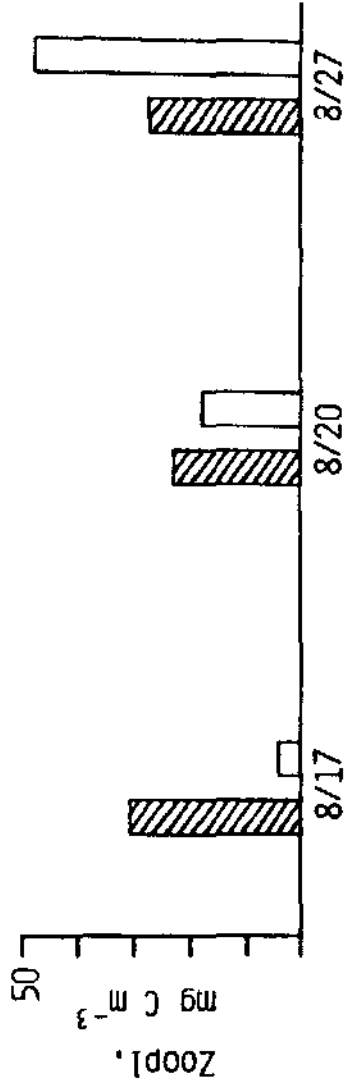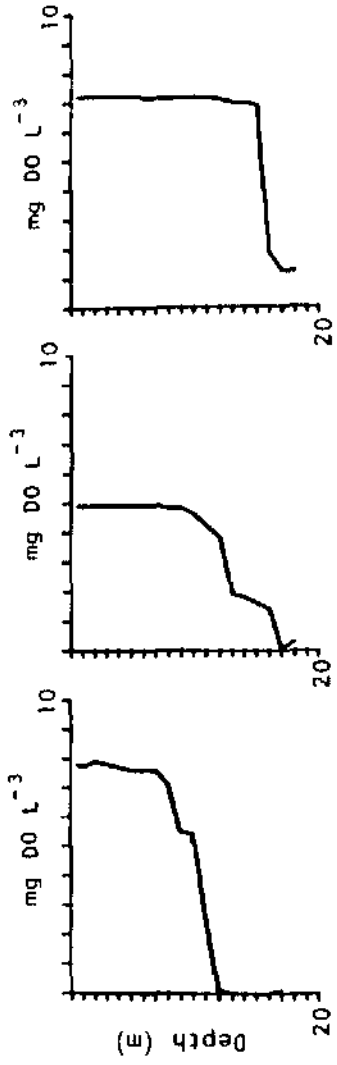
Figure 1b. Same as in 1a for August 17, 20 and 27.
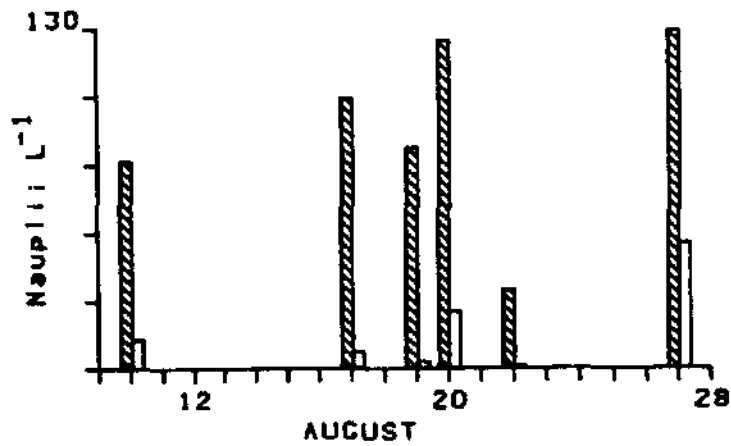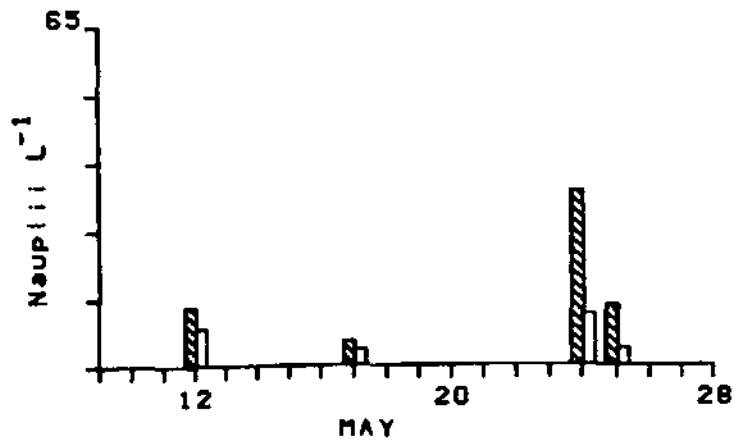
Figure 2. Densities of copepod nauplii at the mid-Bay station in May and August. Shaded bars represent nauplii above the oxycline; open bars represent nauplii below the oxycline.
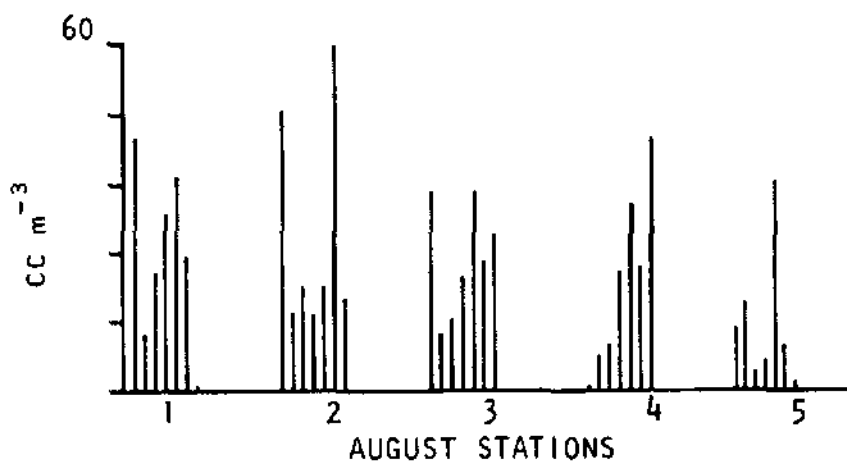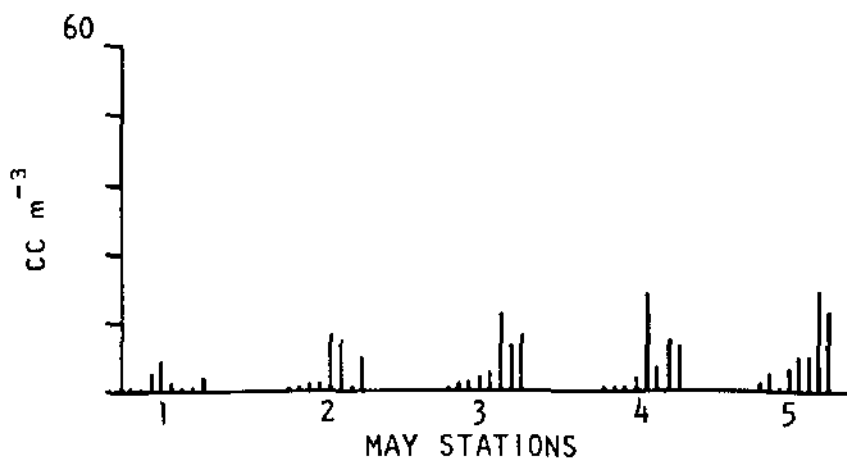
Figure 3. Biomass (displacement volume = cc/m^3) of gelatinous zooplankton (>500 μm) over a two-week period in May (upper) and August (lower), 1986. Sampling transect across Chesapeake Bay off Little Choptank River (5 = Eastern, 3 = Mid-Bay, 1 = Western.

CONTRIBUTION OF SULFUR CYCLING TO ANOXIA IN CHESAPEAKE BAY

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Sulfur cycling in estuaries is a dynamic process involving both the water column and sediments. It is comprised of two key reactions: the reduction of sulfate to sulfide, catalyzed by obligately anaerobic bacteria and fueled by organic carbon from phytoplankton production; and sulfide oxidation, which consumes oxygen and may occur biologically or abiologically. We report here preliminary results of our 1986 studies to:

1. Determine the contribution of sulfide oxidation to oxygen consumption at the O_2/H_2S interface during water column anoxia.

2. Determine whether water column sulfide oxidation is biologically catalyzed or is a strictly abiological reaction.

3. Estimate sulfide flux from sediments to the water column.

4. Relate depth-integrated sediment sulfate reduction rates to hydrogen sulfide flux from sediments to the water column.

5. Determine the factors controlling sulfate reduction in the water column and in Bay sediments.

Anoxia in the Bay in summer 1986 was widespread in the mesohaline portion of the Bay, but persistent anoxia did not occur until mid-July and lasted in our study area (a

lateral transect at the Choptank River) only until mid-August. Because sulfate reduction in the water column can occur only during anoxic events, measurements of water column sulfate reduction were confined to August. Water column sulfide concentrations during 1986 were about two-fold higher than in 1984 and 1985, reaching levels as high as 34 μM. Water column sulfate reduction rates were up to ten-fold higher than observed in previous years with the highest rates (12-20 mmol $S^{2-}/m^2/d$) found at the deepest mid-channel stations. High integrated water column rates were a function of both increased depth of the anoxic zone at these stations and higher rates of sulfate reduction in bottom waters near the sediments. Water column sulfate reduction seems to be limited by available bacterial carbon and energy sources. Addition of lactate to sulfide-bearing waters increased the rate of sulfate reduction by as much as twenty-fold.

Despite high rates of water column sulfate reduction, sediments still dominated total sulfide production. Mean August rates were about 55 mmol $S^{2-}/m^2/d$. In agreement with previous years, sediment sulfate reduction was strongly influenced by temperature with a Q_{10} of about three. However, there also appeared to be an influence of carbon flux, particularly at the shallowest (CP2, Zmax = 8-12 m) of the two sites studied. Sulfate reduction rates were usually higher at the shallow station than at a deeper, mid-channel site (CP3, Zmax = 16-24 m). Nevertheless, depletion of sulfate with depth was most pronounced at CP3, probably due to the tendency of the sediments at this station to remain anoxic during the summer. During August, sediment sulfate reduction at CP3 was likely limited by sulfate below the 4-6 cm horizon. Sulfate was virtually undetectable at 8-10 cm. Pore water sulfide concentrations increased during the summer, reaching a maximum of about 11 mM in mid-August. Pore water sulfide concentrations at CP2 also increased during the summer but remained more than an order of magnitude lower than at CP3, reflecting the fact that surficial sediments at the former site were seldom, if ever, anoxic. Total reduced sulfur in the sediments ranged from 50 to >450 mM.

Preliminary experiments to assess carbon flow through sediment sulfate reduction were done at CP3 in August. Acetate turnover was extremely rapid with turnover times as low as 4 min. and increasing gradually with depth in the sediment. Lactate turnover was also high in the 0-4 cm horizon, but decreased rapidly below 4 cm. Acetate respiration was markedly higher than lactate respiration below 2 cm, suggesting that acetate is preferred over lactate as a carbon and energy source by the sediment microflora. Assessment of pore water organic acid concentrations by GC-EC (determinations currently in progress) will be required to fully evaluate these data.

A series of measurements of sulfide oxidation in the water column were made during the period of August anoxia. Although the results of these determinations have not yet caused us to modify our previous estimates of 9 mg $O_2/l/d$ consumed during sulfide oxidation, the data suggest that maximal rates of sulfide oxidation occur within a narrow range of sulfide concentrations (0.5 to 1.5 μM S^{2-}). Thus, significant rates of sulfide oxidation may be confined to a very narrow depth band (< 1m) over which oxygen and sulfide coexist. Determination of the vertical extent of this region will require greater sampling precision than we have achieved so far.

Measurements of sulfide flux from sediments to the water column, made under benthic domes, agree within experimental error with independently estimated areal rates of sediment sulfate reduction. However, rates of sulfide oxidation cannot be accounted for (by a factor of 3) by combined water column and sediment sulfide production. During our 1987 studies, particular attention will be paid to determining more precisely the depth band over which water column sulfide oxidation occurs, the formation of intermediates of sulfide oxidation which influence the stoichiometry of oxygen and sulfide, and the relationships between carbon flow and sulfate reduction.

RELATIVE ROLES OF BENTHIC VERSUS PELAGIC OXYGEN-CONSUMING PROCESSES IN ESTABLISHING AND MAINTAINING ANOXIA IN CHESAPEAKE BAY

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The primary objectives of this project were to measure and compare rates of oxygen consumption by water-column and benthic processes and to estimate the effect of these processes on turnover of oxygen pools in the bottom water of Chesapeake Bay during spring and summer. Secondary objectives include: (1) measuring flux of sulfide from sediments to anoxic overlying water during summer; (2) partitioning water-column respiration into ecologically relevant size groups; (3) estimating the role of benthic nutrient recycling in maintaining high rates of plankton production during late spring and summer; (4) comparing measurements of oxygen and nutrient fluxes across the sediment-water interface using shipboard incubated intact cores versus in situ chambers.

During the calendar year 1986 water-column and benthic respiration measurements were made at two stations (CP2, 10 m; CP3, 25 m) in mid-Chesapeake Bay (38° 34.3' N) during twelve cruises on the following dates: Mar 27; Apr 4; Apr 11; Apr 18; Apr 25; May 2; May 14; May 18; May 22; June 15; Aug 14-15; Aug 25-26. Nutrient fluxes across the sediment surface were also measured on these dates, and sediment nitrification rates were estimated (by N-Serve technique) on selected occasions. On ten dates water-column respiration was partitioned into three size-groups by

pre-filtration: <3 μm, bacteria and protozoa; 3-64 μm, phytoplankton and small zooplankton; >64 μm, large zooplankton. Sediment-water fluxes of oxygen and nutrients were measured simultaneously using both in situ chambers and shipboard-incubated intact sediment cores on four occasions in May and August. Fluxes of sulfide from sediments were measured at CP3 twice during anoxic summer conditions. Benthic macrofaunal communities were sampled through spring and summer conditions, and animal abundance and diversity have been estimated.

Although data analyses are still in progress, various results are presently available. Some implications of these results have been considered; however, full statistical analyses are incomplete. Benthic oxygen consumption rates were consistently higher at the 10 m station (CP2) compared to the deeper station (CP3, 25 m). Rates at CP2 increased steadily from ca. 1.0 g $O_2/m^2/d$ in April to ca. 1.7 g $O_2/m^2/d$ in August. During the same period benthic oxygen consumption at CP3 decreased from about 0.8 to 0.4 g $O_2/m^2/d$. This marked difference in rates and seasonal trends may be attributable, in part, to the substantially lower abundance of macrofauna at CP3 in spring, with populations decreasing at the onset of hypoxia and being eliminated during summer anoxia. However, measurements of sulfate reduction (by Tuttle et al., personal communication) suggest that there is considerable metabolic activity in the deeper sediments during this period. Direct measurements of sulfide flux from sediments at CP3 during August revealed rates which are stoichiometrically equivalent to the highest oxygen fluxes measured during this study (ca. 1.8 g $O_2/m^2/d$). Thus, it appears that sulfide release from sediments and subsequent oxidation in the water column represents an important oxygen consuming process which has not been previously considered in most oxygen budgets.

Rates of benthic ammonium regeneration were sufficient to supply 30-60% of the nitrogen required by phytoplankton for steady-state growth in spring and summer. In general, ammonium recycling rates followed a seasonal pattern which appears to be strongly correlated to tempera-

ture. However, preliminary analyses indicate that ammonium recycling rates are directly proportional to contemporaneous rates of particulate nitrogen deposition if one applies a temperature-dependent lag-time between deposition and regeneration. Rates of particulate nitrogen deposition exceeded regeneration rates by a factor of 2-3 in spring, but the two processes came into balance in August. During the spring, nitrogen loss via denitrification was estimated to be about one-half of the total nitrogen cycling; however, denitrification approached zero in summer, presumably a result of low redox conditions and associated loss of macrofaunal populations and nitrification.

Respiration rates in surface waters increased steadily from early spring to late summer with warming water temperatures. Rates increased from ca. 0.01 mg O_2/l/h in April to ca. 0.02 in May to 0.035 in August. Oxygen consumption rates in bottom-waters during spring and at the pycnocline during summer were similar to rates in the surface layer. Pre-filtered respiration rate measurements indicated that the organisms < 3 μm consistently accounted for about 45-70% of the total oxygen consumption in surface waters and 70-100% of consumption in bottom and pycnocline waters. The 3-64 μm size-fraction accounted for most of the remaining respiration with a few exceptions in late spring and summer when metabolism associated with larger particles appeared to contribute 10-20% of the total respiration. During one August cruise, pelagic respiration was measured 4-5 times spaced over a 24 h period. Significant diel cycles were revealed with highest rates occurring in morning, and markedly reduced values in late afternoon and evening. This pattern suggests that respiration may be closely coupled to phytoplankton production and that morning respiration rates cannot be directly extrapolated to calculate diel totals.

Preliminary budgets comparing oxygen consumption in water-column and sediments were developed based on several assumptions. These include: (1) the diel pattern of pelagic respiration measured in August is representative of spring conditions as well; (2) benthic oxygen consumption rates at CP2 are relevant for the entire Bay bottom deeper

than 8 m; (3) mean height of the hypolimnion (bottom layer) subject to anoxia is about 8 m. Under these conditions benthic respiration accounted for 48, 39 and 36% of the total oxygen consumption in April, May and August, respectively (where August rates are for oxygen consumed by sulfide released from sediments). Without replenishment, pools of oxygen in this bottom layer would be consumed (by all metabolic processes combined) within 30, 10 and 1 days in April, May and August, respectively. Thus, biological respiratory processes in late spring and summer are capable of rapid depletion of oxygen in bottom waters of the Bay, and both water column and benthic communities play an important role in creating and maintaining anoxic and hypoxic conditions.

DISCUSSION

Fisher: I had been asked earlier about ammonium regeneration in the water column and in the sediment. Mike Kemp just provided some numbers for ammonium regeneration and I just made a back-of-the-paper calculation to make sure that oxygen consumption in the water column and the sediments was at least the same order of magnitude, if you accept his assumptions. If you make the same computations for ammonium regeneration you get numbers which are again the same order of magnitude. That is, there is some sort of equal partitioning of the ammonium production per square meter in the subpycnoclinal waters and in sediments, or within a factor of 2 to 5 of the same order of magnitude. So that goes along with the story that the matrix is showing for oxygen.

Mountford: Mike, am I reading you correctly, that the sediments are not serving as a major cumulative sink, but that you are getting processing of what comes in, that is a reasonable steady state over the period of an annual cycle?

Kemp: Yes, that's my feeling. There is some burial, and there is this lag, particularly between deposition that occurs in the spring or in the late winter. There is a lot of phytoplankton production occurring in the later winter/early spring. Some of that is deposited, and it's consumed at a very low rate in the sediments. There is very little accumulation in the sediments. In fact, according to Scott Nixon's nutrient budget of the Bay, I guess there is not enough.

Boynton: The particulate carbon profiles look pretty straight, once you get down below the surface layer. It's mostly a surface phenomenon, and seasonally up to an annual period I think most of what gets there goes away; lags during cold seasons, less lags during the very warm seasons.

Mountford: So, once we are able to establish more oligo-trophic conditions in the Bay, then you wouldn't have some terribly long memory to contend with.

Boynton: My initial feeling was that the sediments would [have a memory] but based on experiments we have done, I think that for nitrogen anyway there is not a long memory. At this point, I would defend that point of view more than I would defend the opposite one.

Mountford: What about phosphorus?

Boynton: I don't know. I'm am waiting for someone to discover a gaseous phase and we would be off to the races.

Kemp: I should add a disclaimer to that, Kent -- Walt Boynton and I published a paper a few years ago that said that there was an excess amount of carbon left over in the fall that didn't get consumed. We conceived that this might provide food for spring recruitment of benthic invertebrates. We published that based on some reasonably good estimates, but now I doubt that it in fact holds. I think it is mostly what is produced in the spring and the summer that supports the secondary production.

Malone: What I want to know is once we add these hetero-trophic processes up, can we still consider this a phyto-plankton-driven system?

Ducklow: One comment -- once you see all this carbon go into the bacteria, people may ask how there can be any left over for anything else. Which makes the point that a lot of what the bacteria get comes via other heterotrophic pro-cesses, especially grazing. They are not at all mutually exclusive, and they aren't simply additive.

Tuttle: But if it doesn't come directly from the phyto-plankton, it's even harder to justify because it means it is going up a couple of trophic levels and still coming mostly through the bacteria. The most efficient way to explain it is that it's coming directly from the phytoplankton.

Ducklow: I don't think there is a lot of evidence that a large part of the bacterial production is coming that way.

Tuttle: I know. And if your bacteria are taking over 100% and so are the microzooplankton, and you still get hypoxia in the sediments and we still catch a few fish, we all better go home to flush our toilets to keep the system going -- because the phytoplankton aren't doing it!

Comment: It seems like we have two problems: Tom Malone is showing data for accumulation of phytoplankton below the pycnocline -- the accumulation of phytoplankton production creating an oxygen demand. On the other hand, looking at the grazing numbers, we are apparently consuming too much of the phytoplankton. The bacteria and microzooplankton are sometimes consuming greater than 100%.

Ducklow: But not in the spring [general agreement].

Sellner: When I just went through these numbers, the total grazing pressure by both our groups -- but not bacteria -- would be about 30% in the spring.

Comment: So that would leave 70%. That's still consistent then.

Kemp: That is exactly the respiration that we got for bacteria.

Question: Jon Tuttle has said that sulfur oxidizers are using up a lot of oxygen — Jon, how much carbon are they fixing?

Tuttle: I didn't say sulfur oxidizers were doing that. So far our data suggest that most of the sulfide oxidation occuring in the water column is truly chemical. After postulating five years ago that there ought to be a substantial chemo-autotrophic-bacterial production in the water column or in the sediments or some place with all the H_2S being formed -- over five years I haven't got a single shred of evidence that suggests that is the case. So I have changed my mind.

Jonas: There might be other sulfur intermediates that might persist longer up in the oxygenated water column, which could conceivably be consuming oxygen elsewhere, so there may be a sort of hidden residual sulfur demand.

Tuttle: What you are suggesting is what we see in some oceanic environments, which is a carbon-sparing effect. That may be occuring; we haven't taken a look at it. There are in fact heterotrophic bacteria in the Bay that will oxidize some of the partially oxidized sulfide intermediates. In fact, you may be conserving carbon so that we end up getting estimates like Hugh Ducklow has made that the bacteria are eating all the carbon. Now maybe they (sulfur oxidizers) are simply conserving carbon, I don't know.

Comment: That was the point I was getting at. So what you are saying is that there is some potential for carbon fixation.

Tuttle: But what you are implying is chemo-autotrophic primary productivity and I don't see that as an enormous factor.   I don't think that can solve the dilemma that we have.

Mackiernan: No hydrothermal vents, eh?   What are some of the response, turnover rates, or reproductive rates of some of those micrograzers?   They can respond more quickly than copepods.

Brownlee: In some cage culture experiments we got turnover rates of about 8 hours in August, for several sized species — both large and small.

Mackiernan: Those organisms are probably themselves grazed upon by jellyfish.

Brownlee: And mesozooplankton.

Roman: Most of the copepod species are omnivores — you can grow them on the tintinnids and other microzooplankton that Dave Brownlee and Kevin Sellner look at.   Data on zooplankton and microzooplankton show sort of an inverse relationship.

Sellner: What we plan to do this summer are some more cage cultures with the dominant microzooplankton species and see if in fact we can get an ungrazed maximum growth rate, more or less. So we would have a better estimate of total microzooplankton turnover demand, versus a doubling time for phytoplankton of once every two days or once every day.

Question: What stimulated you to plot microzooplankton grazing versus dinoflagellate biomass?

Sellner: We were looking through some of our data and found Favella as one of the dominants, and Stoecker at Woods Hole Oceanographic Institute has reported this ciliate as a dominant grazer in red tides in New England. Therefore, we thought there might be a relationship between dinoflagellate biomass and microzooplankton grazing pressure in the Bay. When we tried to establish any other relationship between total microzooplankton density and any standing crop measure, nothing fell out; it was absolutely random. One that did appear to suggest that there might be some response of the total microzooplankton community was biomass of the dinoflagellates.

Haas: Were you counting cyanobacteria?

Sellner: Yes, but not with epifluorescence techniques.

Haas: In lower Chesapeake Bay one can observe coccoid cyanobacteria at almost a million per milliliter -- substantial numbers.

Sellner: Yes, we have values like that, but we never stressed them because, again, we are stretching the limits of our taxonomists. . . (hard to see and identify).

Mountford: Do microzooplankton eat picoplankton or, more specifically, cyanobacteria?

Brownlee: We found significant grazing on bacteria as well as phytoplankton. Some species, such as Synchaeta, also showed a higher clearance rate on bacteria than phytoplank-

ton -- in terms of ingestion, it was greater than 50% on bacteria. Most other species concentrated on phytoplankton.

Sellner: It was almost always autotrophic-dominated, in terms of ingested carbon.

Mountford: So in that sense the picoplankton or cyanobacteria may be sort of "waste production?"

Sellner: Well, we are going to do some size fractionation to actually look at the prey for the various microzooplankton, for instance the tintinnids Dave Brownlee was talking about, to get a better idea of what each size group is eating.

Nixon: Has anyone put together a good inventory of allochthonous carbon inputs into the Bay? I have not seen one. I don't think USGS or EPA did carbon in their studies. A surprising omission.

Malone: I think it would be pretty low, Scott, relative to autochthonous production.

Nixon: But we haven't done it yet; it is hard to know.

Malone: We could probably estimate that, given river discharge rates, DOC levels, TOC, etc.

Kemp: The Biggs and Flemer article on carbon budgets done way back gave estimates on a rough level.

Malone: That was all POC, though. But if the POC was mostly autochthonous, it's hard to see that the DOC would be allochthonous -- it's more labile.

Houde: I'd like to suggest an idea that we might want to consider, especially in light of the papers tomorrow. There is a controversy going on about the eutrophication of the Great Lakes, and the causes of that -- this centers on what is essentially the concept we have been talking about today -- that nutrient inputs stimulate primary production or increases in algal biomass and sedimentation and oxygen

demand -- the "bottom-up" concept versus the "top-down" concept that alterations in grazing pressure -- harvesting of oysters or fish -- is essentially decoupling primary production from secondary production, and what you then get is a higher accumulation of algal biomass with or without changes in the nutrient loading rate. There's understandably a controversy in the Great Lakes between the fishery people who think it's removal of the fish that's causing the greening of the lakes, and the nutrient chemists who think it's the nutrient loading. We should think about that in the context of the papers tomorrow -- for example, Roger Newell raised the issue of oyster grazing and effects of decreasing oyster populations -- we might want to consider whether the accumulations of algal biomass leading to hypoxia in deep waters is the result of increased phytoplankton productivity and biomass or the result of the decoupling of that production to secondary productivity. There is the interesting potential link between water quality anf fishery yields: if you increase the nutrient loading you can divert that into higher fish production or you can decrease water quality, depending on whether that is coupled or decoupled.

Tuttle: I think you've hit on something here. It looks to me as if there has been a basic change in the ecosystem of Chesapeake Bay. Now, one possible explanation for that is that there are too few oysters or too few striped bass or whatever, and what we've done is simply throw it into this phytoplankton-bacterial loop.

Newell: But if 80% of the production is by species smaller than 3 microns, a lot of macroinvertebrates can't filter such small particles efficiently. Perhaps only micropredators can capitalize on those small cells.

Sellner: Interestingly enough, the largest productivity max is when the small cells dominate.

Jonas: You bandied about this concept of a positive feedback loop. Once you knock the oxygen down to a certain level, it might have this impact so that even if it's not wiping them out, it is selecting certain groups, and all of a sudden you have flipped it over into this phytoplankton-

production, microheterotroph-respiration system, which for all intents and purposes looks like a waste water treatment plant. It is an aged trophic community from the bacterial point of view, which is very good at utilizing oxygen and producing some sludge. And that is what we are looking at.

Comment: As much as I hate to say it, it is like an alternate steady state for an ecosystem. You can either go to a respiration system or you accumulate phytoplankton biomass on the bottom and it consumes oxygen there or you in fact send it through a trophic structure that results in oysters and fish and so on, which is what we're all trying to do.

Jonas: Hugh, are you familiar with any systematic bacterial abundance historical records for the Great Lakes? In terms of eutrophication there versus a place like the Bay?

Ducklow: "History" for good bacterial abundance measurements is the last ten years. But interestingly enough, Don Scavia at the Great Lakes lab is doing the same work in Lake Michigan, which is a cleaner, more oligotrophic system, and he has the same problem with bacterial production versus phytoplankton that we do here. The absolute levels are lower, but he is having trouble finding out where it comes from as well.

Biological Effects
of Hypoxia

DEPICTING FUNCTIONAL CHANGES IN THE CHESAPEAKE ECOSYSTEM

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The usual method of studying ecosystems' response to perturbations such as hypoxia has been to create simulation models of the system dynamics. Models require copious data on species stocks and intercompartmental flows. It is possible to extract much information useful for deciding management issues from the structure of the exchanges itself, without having to invoke the manifold a priori assumptions required for simulation. One modeler has likened simulation modeling to studying the "physiology" of the ecosystem, whereas flow analysis is akin to inspecting the system's "anatomy" (Figure 1).

Flow analysis can be made at several hierarchical levels. For example, one may calculate the total exchanges between any pair of species over all direct and indirect pathways. In this manner, one may portray the "extended diets" of species of interest. For example, the striped bass is known to directly ingest bay anchovies, menhaden, crabs and alewives. But these prey in turn consume a host of other invertebrates and plants, some of whom feed on still others, etc. Using matrix and vector operations it becomes possible to calculate the extent to which any organism of interest depends upon any other compartment for direct and indirect sustenance (Table 1). Although adult striped bass do not feed on zooplankton directly, the latter item has been incorporated into about 67% of the striped bass prey. The extended diets of adult striped bass and bluefish are seen to diverge in that bluefish are indirectly more dependent upon benthic materials and organisms than are the

striped bass. Hence, bluefish diets are more likely to be impacted by anoxic events.

Similar matrix operations allow one to determine the average trophic distance over which each feeding organism obtains its food (Table 2). In the Chesapeake system, despite the existence of some feeding pathways with as many as eight trophic links, no carnivore feeds, on the average, at trophic level 5 or higher (Table 3). If this assignment represents "the apportionment of integral trophic levels among the species," then it is interesting to note that the inverse operation is also possible. That is, knowing the various trophic pathways along which food reaches a particular species, one can divide the activity of that species among the integer trophic levels in proportion to the intensities of the pathways of various lengths. The end result is to transform the arbitrarily complicated network of exchanges into a "straight chain" of ever-decreasing transfers -- the classical Lindeman trophic pyramid. The effects of stresses such as hypoxia are most likely to be exhibited as changes in the upper trophic elements of the chain. Any abrupt change in the trophic assignment of a particular species would probably indicate a strain on that organism. One of the outgrowths of the trophic aggregation exercise in Chesapeake Bay is the revelation that detritivory and saprophagy exceed herbivory by ninefold, thus underscoring the potential of anoxic events to modulate heterotrophic productivity in the Bay.

Control in the ecosystem is usually indicated by feedback cycles of material and energy. Such cycles inherent in the web of exchanges can be enumerated and extracted from the network using an appropriate backtracking algorithm. The pattern of feedback in the Chesapeake system is bipartite with recycle among the pelagic species decoupled from feedback among the benthic and nektonic components. The entire suite of filter-feeding organisms engage in no feedback, but rather perform the function of shunting material and energy from one domain of control to the other.

Finally, it is possible to characterize the development stage of the overall network using techniques borrowed from information theory and flow analysis. In particular, if one has access to the configuration of the system at two or more different times, it becomes possible to quantitatively verify the existence of heretofore qualitative phenomena such as eutrophication and ecosystem "health."

A preliminary quantification of carbon exchange among the 35 major components of the mesohaline ecosystem during each season has been made. Work is currently underway to compare the structure of the Chesapeake network with a similar study of the Baltic Sea being conducted by the ASKØ laboratory of the University of Stockholm.
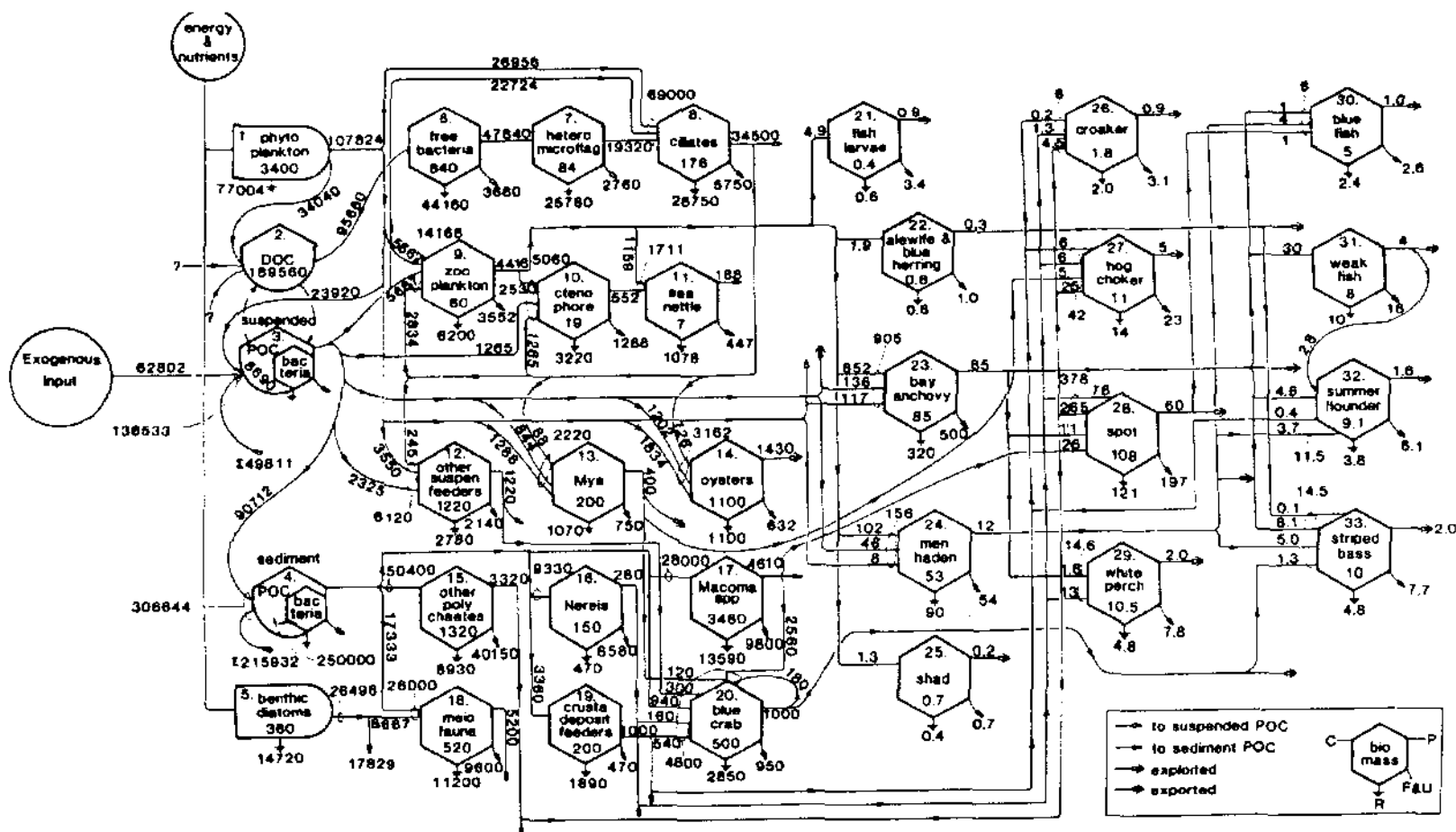
Figure 1. Flow diagram of Chesapeake Bay mesohaline ecosystem in summer months, showing direction and magnitude of carbon exchanges

Table 1: Matrix of total dependencies (species numbered as in Figure 1). Column Values represent the present direct or indirect contribution of each row species to the diet of the species represented by the column. For example, phytoplankton (1) contribute about 65% to the diet of sea nettles (11), primarily through indirect pathways.

	23	24	25	26	27	28	29	30	31	32	33
1	.6742	.6069	.6759	.5731	.5943	.5761	.5842	.5976	.6742	.6490	.6434
2	.1083	.1205	.1210	.0700	.0696	.0711	.0742	.0855	.1083	.1108	.1091
3	.4851	.5987	.4647	.4962	.4839	.4959	.4950	.5112	.4851	.5220	.5243
4	.0	.0	.0	1.0000	.8810	.9709	.8904	.6473	.0	.0348	.0815
5	.0	.0	.0	.1216	.1071	.1181	.1083	.0787	.0	.0042	.0099
6	.1083	.1205	.1210	.0700	.0696	.0711	.0742	.0855	.1083	.1108	.1091
7	.0933	.1021	.1067	.0548	.0547	.0559	.0590	.0698	.0933	.0948	.0930
8	.2664	.2862	.3113	.1405	.1412	.1442	.1543	.1882	.2664	.2684	.2623
9	.7261	.6649	1.0000	.0217	.0208	.0422	.0989	.2599	.7261	.6819	.6437
10	.0058	.0071	.0055	.0062	.0060	.0062	.0062	.0063	.0058	.0062	.0063
11	.0018	.0022	.0017	.0029	.0027	.0028	.0027	.0026	.0018	.0020	.0020

Table 2: Apportionment of Species among Discrete Lindeman Trophic Levels

Level	Phytoplankton	DOC	Susp. POC	Susp. POC Bact.	Sed. POC	Sed. POC Bact.
1	1.000	1.000	1.000	.0	1.000	.0
2	.0	.0	.0	1.000	.0	1.000

Level	Benthic Diatoms	Free Bacteria	Hetero. Microflag.	Ciliates	Zooplankton	Ctenophores	Sea Nettles
1	1.000	.0	.0	.0	.003	.0	.0
2	.0	1.000	.0	.700	.774	.236	.002
3	.0	.0	1.000	.020	.164	.577	.600
4	.0	.0	.0	.280	.004	.087	.297
5	.0	.0	.0	.0	.056	.072	.031
6	.0	.0	.0	.0	.0	.028	.061
7	.0	.0	.0	.0	.0	.0	.009

Level	Misc. Susp. Feeders	Mya Arenaria	Oysters	Misc. Polychaetes	Nereis	Macoma Spp.	Meiofauna
1	.0	.0	.0	.0	.0	.0	.0
2	.936	.937	.0	.0	.0	.0	.333
3	.052	.051	.051	1.000	1.000	1.000	.667
4	.001	.001	.001	.0	.0	.0	.0
5	.011	.011	.011	.0	.0	.0	.0

Level	Crustacean Deposit Feeders	Crab	Blue Larvae	Fish & Herring	Alewife Anchovy	Bay Menhaden	Shad
1	.0	.0	.0	.0	.0	.0	.0
2	.0	.203	.003	.003	.272	.329	.003
3	1.000	.085	.773	.773	.566	.525	.773
4	.0	.710	.164	.164	.118	-107	.164
5	.0	F.001	.004	.004	.004	.002	.004
6	.0	.001	.056	.056	.040	.037	.056

Level	Croaker	Hogchoker	Spot	White Perch	Bluefish	Weak-Fish	Summer Flounder	Striped Bass
1	.0	.0	.0	.0	.0	.0	.0	.0
2	.0	.0	.0	.0	.0	.0	.0	.0
3	.0	.112	.008	.030	.100	.272	.215	.284
4	1.000	.887	.987	.952	.187	.566	.496	.510
5	.0	F.001	.003	.013	.696	.118	.220	.168
6	.0	.001	F.001	.003	.003	.003	.030	.002
7	.0	.0	.001	.004	.013	.041	.029	.036
8	.0	.0	.0	.0	.001	.0	.010	.0

Table 3: Trophic rankings and average trophic levels of the major components of the Chesapeake mesohaline ecosystem

1.	Phytoplankton	1.00	19.	Nereis		3.00
2.	Dissolved Organic Carbon	1.00	20.	Macoma spp.		3.00
3.	Suspended POC	1.00	21.	Crustacean		
4.	Sediment POC	1.00		Deposit Feeders		3.00
5.	Benthic Diatoms	1.00	22.	Ctenophores		3.08
6.	Suspended POC Bacteria	2.00	23.	Fish Larvae		3.36
7.	Sediment POC Bacteria	2.00	24.	Alewife and Blue		
8.	Free Bacteria	2.00		Herring		3.34
9.	Misc. Suspension Feeders	2.09	25.	Shad		3.34
10.	Mya arenaria	2.09	26.	Blue Crab		3.51
11.	Oysters	2.09	27.	Sea Nettle		3.58
12.	Zooplankton	2.34	28.	Hogchoker		3.89
13.	Ciliates	2.58	29.	Weakfish		3.97
14.	Meiofauna	2.67	30.	Croaker		4.00
15.	Menhaden	2.89	31.	Spot		4.00
16.	Bay Anchovy	2.97	32.	White Perch		4.00
17.	Heterotrophic		33.	Striped Bass		4.00
	Microflagellates	3.00	34.	Summer Flounder		4.19
18.	Misc. Polychaetes	3.00	35.	Bluefish		4.64

BIOLOGICAL MONITORING OF SELECTED OYSTER BARS IN THE LOWER CHOPTANK RIVER

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As part of a cooperative project to investigate the possible impacts of anoxic and hypoxic water on Choptank River oyster survival, six oyster bars were monitored weekly during the summer of 1986. To determine survival rates, 60 (sometimes fewer) adult oysters were collected by dredging and classified as either live, newly dead (new box), dying (gaper), or formerly departed (old box). Presence and abundance of yearling spat and selected taxa of fouling organisms were recorded from a subsample of 10 oysters weekly at each bar (Figure 1). Temperature, conductivity, pH, dissolved oxygen (DO) and secchi depth were measured at the surface, mid-depth, and bottom of the water column.

Total mortality, averaged over all sampling periods, ranged from 3.3% on Sandy Hill bar to 35.2% on France bar (Figure 1). There were significant differences in percent mortality among bars, with those closest to the confluence of the Choptank River and Chesapeake Bay having the highest proportions of both old and new boxes. Levels of new mortality were low, with no clear mortality "events" having occurred during the summer. However, abundance and viability of spat correlated positively with the viability of adult oysters. Variations in the abundance and viability of fouling organisms were observed, but these data require further analysis.

No occurrences of anoxia were recorded, and hypoxia was minimal, with the lowest DO values between 3-4 ppm. DO was strongly correlated with pH (Figure 2), but not with either salinity or temperature, suggesting that DO varia-

tions were driven primarily by photosynthesis in the relatively shallow (3-6 m) waters over the oyster bars. High levels of old mortalities at the downstream bars may have resulted from hypoxia during previous summers, from disease or other causes. This study was designed to capture short term mortality events which did not occur to any significant degree during the summer of 1986. Monitoring will continue in the summer of 1987 with the addition of an oyster pathology component. Complementary hydrographic studies conducted by DNR and the University of Maryland, Horn Point Environmental Laboratories, will continue to investigate the hydrodynamic aspects of DO dynamics in the lower Choptank River.
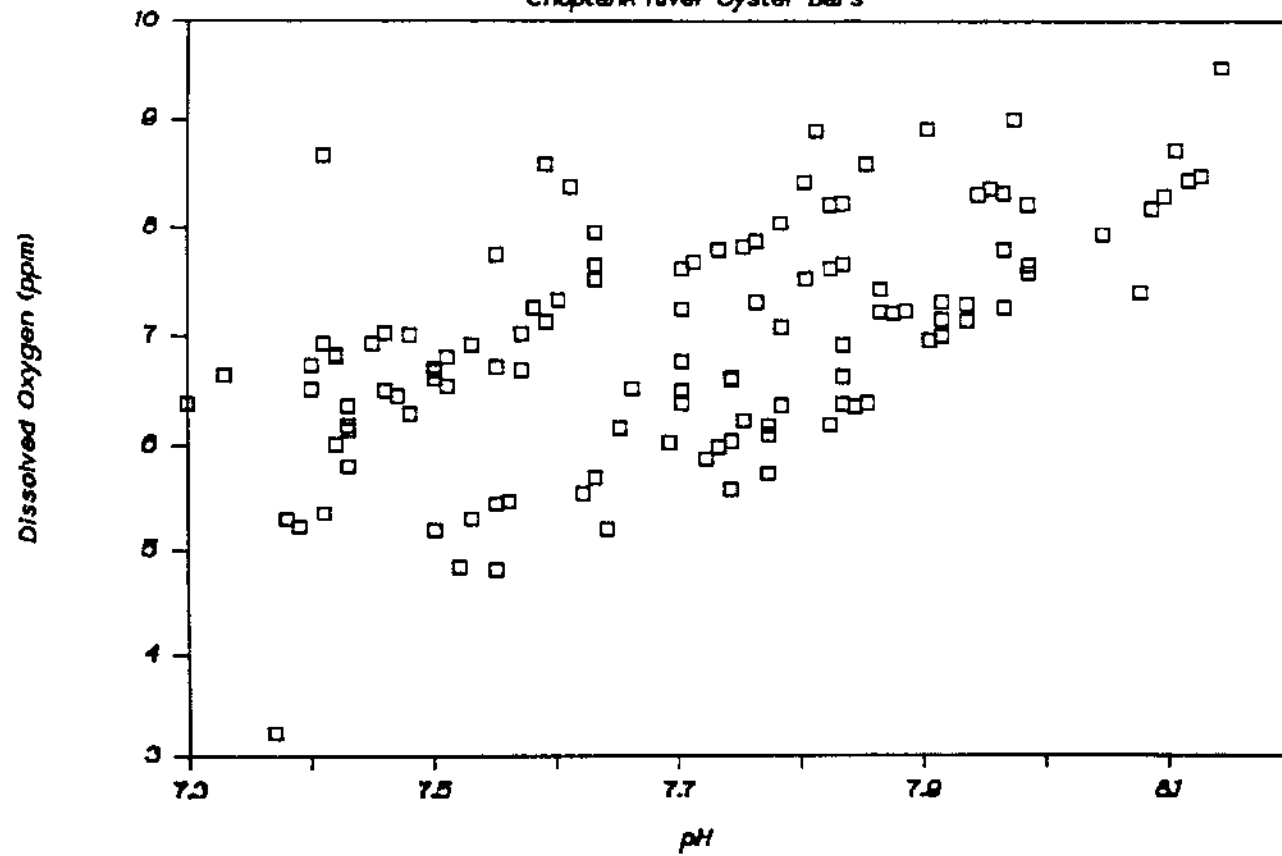
Dissolved Oxygen Versus pH at 6

Figure 1. Dissolved oxygen concentrations versus pH at six Choptank River oyster bars.
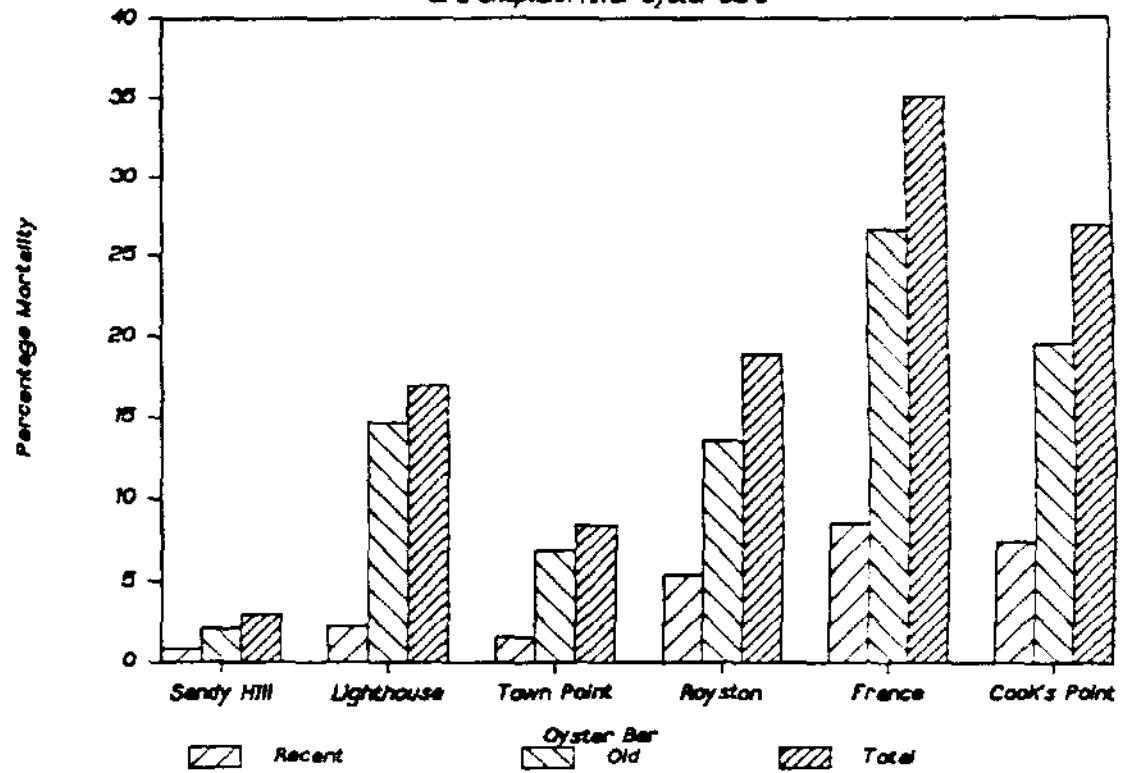
Total, Recent, and Old Mortality

Figure 2. Total, recent and old mortality at six Choptank River oyster bars.

DISCUSSION

Roman: How persistent was that low oxygen feature in the upper reaches of the Choptank?

Jordan: The continuous monitoring was not long-term last summer, but a preliminary look at data from grid surveys indicates that it's reasonably persistent. In 1984 I had essentially anecdotal evidence that DO was extremely low, 0.3 mg/l in shallow water, at 4-5 m depth. I think what we're looking at are very short-term events that could potentially impact the shallows. That's what we're trying to find. . . .

Newell: There is good evidence that adult oysters can withstand 5-7 days of anoxia or longer, depending on the temperature. I don't think anything has been presented so far at this session that suggests anoxic events persist for this long in shallow water, even on the Western Shore, in areas where you've got extensive oyster bars today.

Question: Did you look at fouling organisms, bryozoans, etc., which might be more sensitive to low DO to see if there was any evidence of mortality?

Jordan: We did look at fouling organisms and the data haven't been analyzed yet. We also looked at year-old spat and there was a pretty good correlation with spat survival and DO in this downstream area. So something is impacting these downstream bars and it looks like a DO problem. Whether low DO is the cause, or simply interacting with disease or some other stress, we don't know.

Newell: That of course is the major question. There are several diseases, such as MSX, which are positively correlated with salinity and could also be affecting the oysters.

Question: Do you know anyone who has been able to distinguish specific causes of mortality in bivalves?

Jordan: This would be difficult to do from any field monitoring program because you don't actually see them die. We are now looking for habitat factors which could potentially impact resources, and to do that, we go out in the field and look for correlations. When we find correlations, then it's time to support more detailed work and look at cause-and-effect.

Kennedy: When you go out and bring in some dead oysters, and find relatively large live barnacles on their shell, then it's probably not oxygen, it's probably disease.

Question: Could it be H_2S?

Kennedy: But would we expect the fouling community to be less sensitive to this than the oyster? In other words, if you have a community, and the oyster bed community is a very diverse one, and if all that's dead is the oyster, then I thnk you're looking at an oyster-related problem, not an ecosystem problem.

Jordan: That's why we are going to look very hard at our fouling data, using multivariate techniquest to discriminate among the bars and their fouling communities. If we see healthy, old fouling communities associated with dead oysters, then it is probably an oyster problem, not oxygen.

Question: What is "old mortality?"

Jordan: This is a pretty standard technique in Maryland. You dredge the sample, and looking only at articulated shells, if there's fouling inside the shell, that's an "old mortality." If the shell is clean, that's a "new mortality."

Question: No real time scale then?

Jordan: No, but for this study we consider that the mortality was from about a year before. I hadn't planned to get into temporal trends, but there was some indication that we saw higher levels of new mortality early in the season, in June, and increasing numbers of old mortality later. This

says that perhaps there was a mortality event in the spring before we got out there, and there's been a suggestion that could have been due to disease.

Mackiernan: For an oyster that is operating anaerobically, how long can it go without depleting its glycogen? These anoxic events aren't continuous, but can be frequent and there may not be much reaeration in between.

Newell: An oyster held out of water can stay closed up 5 days or so at high temperatures, for 2-3 weeks at low temperatures. A couple of days of reaeration between anaerobic events should be OK; they have sufficient nutrient reserves to withstand a day or so of anoxia with a few days aeration in between. It is obviously going to be a stress eventually, because these energy reserves should be used for gametogenesis. So you have a possibility of impacting the whole population by affecting reproductive success. At one time it was thought that bivalves in general had a very inefficient anaerobic metabolism, but now we know that is not true. In fact, it is highly efficient and highly evolved, so we must not think that anaerobiosis is necessarily any great stress.

Jordan: In fact, intertidal oysters spend a great deal of time closed up, and do just fine.

Mann: If you believe the work the Dutch have done with mussels, and in fact also shown in some of Charlotte Mangum's work, the oyster functions to some extent anaerobically all of the time, irrespective of the oxygen environment. And that brings up another question which has not really been addressed by anyone in this group yet; that is, a significant part of the benthos consists of organisms which are evolved to function in low oxygen environments, and if the Dutch work can in any way be transferred to the rest of the animals that live in the benthos, there is a suggestion that a part of that benthos functions, in part, anaerobically all the time. Then what you are getting into is carbon and nitrogen cycling that has nothing to do with oxygen cycling at all. So when we consider trying to do mass balances functioning in terms of N or C, and assuming that oxygen

runs in parallel, we may in fact be making a mistake once we get into the benthos.

Comment: That gets back to what we were talking about yesterday: there is a big difference between just a small amount of O_2 and complete anoxia, because a concentration of 0.1 mg/l is still enough to provide some aerobic respiration for the benthos.

Newell: I don't want people to think that low O_2 and hypoxic conditions aren't a stress on the oyster -- they are. An oyster can withstand it, but its feeding activities are compromised during this time, and according to its overall energy budget, it's going to be compromised. That is why it's important to consider the effects into the next generation.

Mackiernan: I think that in some of the REMOTS camera work that was done in the Bay for the Corps of Engineers, the photos showed that in areas where there were considerable repeated anoxic events the benthic community was essentially limited to opportunistic species which recruited in the winter, and there were no normal deep-living polychaetes and such. Obviously there is at least gradual attrition of the benthos.

Kemp: You can see that along a water-column depth gradient anywhere in the mesohaline Bay.

Mackiernan: True. In fact some people have looked at old cores from areas that are now anoxic in most summers and found large Macoma valves, which being rather a long-lived bivalve, you would not expect to have survived if anoxia were a common occurrence in the past. But no one has really pursued that.

Newell: I would like to ask Bob Ulanowicz a question. He seemed to show that the suspension feeders were the important links between the water column processes and the higher trophic levels, such things as Mya and Macoma. What were the links from those bivalves into the higher levels?

Ulanowicz: The link between the filter-feeding bivalves were primarily blue crab and also such nektonic species as hogchoker, spot, white perch and so forth.

Newell: That just emphasizes the importance of the suspension feeding invertebrates in the overall nutrient cycling within the Bay.

Comment: In aerobic waters. . . .

Ulanowicz: Also, they are taking a lot of suspended POC out of the water column and putting it into the sediments. A major function.

Kemp: Well, from what I know in the main area of the Bay (in Maryland) which goes anoxic, Macoma balthica is the dominant species by biomass, and here at least it is not a suspension feeder, it is a deposit feeder. Where (or what) are all of these suspension feeders, besides oysters? And Mya in the fresher areas.

Jordan: Barnacles. . . .

Kemp: But that is part of the oyster community. Most of the area that we are talking about is soft-bottomed community.

Comment: Well, there are amphipods, polychaetes. . . .

Purcell: I have a question for Bob -- have you tried to incorporate certain complex life histories into this model at all so that you have both planktonic and benthic stages of these animals, or does that complicate the model so that it is unworkable?

Ulanowicz: They are combined, with the exception of fish larvae, which we did distinguish because of their different feeding patterns and their importance later on. That still complicates what you have, because if the feeding habits of life stages are different, then your component here will have a more complicated multiplicity of inputs. I will say that what you are looking at is just for the summer. We are

now essentially making seasonal snapshots for the four seasons so we will have some idea of the temporal variation in this particular network. I think Gail Mackiernan asked earlier what would happen if you removed species "23" or "x" or. . . . There are a couple of things you could do. You could look along row 23 for large numbers in that row, indicating a strong direct or indirect independence on that species, which would immediately alert you to a potential problem. There is also a form of sensitivity analysis which can be run on the topographical model alone -- we have those algorithms available. So if "23" no longer feeds on "15," we can determine quantitatively how that affects the network. I will also add that most of the software is available for the IBM PC, and is rather easy to use.

Jonas: This is a mesohaline model -- could you put some geographic limits on what you think it applies to?

Ulanowicz: It's approximately from the surface 6 ppt iso-haline in the north down to about the surface 18 ppt iso-haline. Geographically, that's a little bit below Pooles Island to just below the mouth of the Potomac. It's about roughly half the surface area of the Bay waters.

Comment: There was a recent study done in Europe showing that Macoma balthica can either suspension or deposit feed quite well.

Kemp: But I don't think it does here.

Comment: Under highly turbid conditions they can switch over to suspension feeding. I want to make a point that in the lower Bay's higher saline waters, we don't have signifi-cant Macoma balthica populations. So during low DO events we essentially lose all our fauna -- they are just completely wiped out. So the benthic community in deep basins where they have significant hypoxic events consists of very shallow dwelling, short-lived organisms, no perennials at all.

Kemp: We have the same situation in the areas Bob Ulanowicz was describing.

Malone: Bob, how did you come up with the exogenous organic inputs?

Ulanowicz: Let me defer to Dr. Baird, who essentially put this together.

Baird: We just tried to balance that particular component, and since it had to come from somewhere else, and was not generated within the mesohaline area, we assumed it had to come from outside.

Malone: In other words, the heterotrophic demand exceeded the primary productivity inputs and so you put that into the balance? That's interesting in the context of what we were discussing yesterday.

Jonas: In that context (from yesterday), in that DOC pool one of the questions is how much of that pool is labile biologically, and how much of it is that refractory "yellow stuff" floating around out there. How might that drive the system?

Baird: We don't really know.

Kemp: But that doesn't really matter with this model, except for calculating turnover rates or the like.

Ulanowicz: The labile portion is seen in that transfer from pools 2 to 6 for the most part. The entire stock is listed under "DOC," 189,560 mgC/m^2 in the water column. The turnover rate is rather slow; most of the turnover being due to the labile fraction. There is some smearing due to the aggregation of the labile and nonlabile fractions.

Jonas: It would suggest, looking at that rate, that something like half the DOC might be labile. I have no idea if that's a high number.

Ulanowicz: Remember this is per summer, per 92 days, not per day. So you are talking about half being turned over in three months.

Jonas: I'm just looking at that box on DOC and looking at that rate up to pool 6 -- the bacteria. If we think the Bay is an unusual system, how much of that DOC is labile compared to the total that is there, and is the Bay really very different than other estuaries in that regard? That is, in that proportionate basis of dissolved matter which presumably has to move through this microtheterotroph community. Is that a driving force? I don't have a simple answer.

Newell: I would like to get back to Bob Ulanowicz's point about the DOC. Perhaps because the estuary is being flushed, the refractory DOC is being pushed out onto the shelf so you only have DOC that is relatively labile and fairly new getting recycled. So maybe you are right — maybe it is fairly labile.

Jonas: Some of the turnover rates (these rates do have some uncertainty) for dissolved organic pools -- glucose for example -- are in the order of two hours for turning over the whole pool on the basis of some data that we have. There is more than one explanation for this, but they do appear to be very high. Up until 1986, our amino acid turnovers -- we were using this mixed amino acid composition that supposedly resembles a phytoplankton protein hydrolysate -- were always much lower than the glucose pool, which surprised us initially because we would assume that the Bay looked more like an ocean system where traditionally the people who play this game think amino acids are a preferred pool. But in the Bay we are leaning towards carbohydrates. That is why I brought up yesterday the question that we may really need to get some information on amino acid composition and quantitation, as well as carbohydrates in that dissolved organic pool.

Ulanowicz: Appropos your earlier comment as to how this compared with other estuaries, I am not an expert on DOC dynamics, but we are endeavoring to contrast this network with a very similar one in the Baltic that the ASKØ lab is developing, and hopefully in a few months will be able to say something about the section of the network with respect to

the turnover rates of DOC pools here and in the Baltic and also their relative importance.

Jonas: From the point of view of the heterotrophic microbial community, we have in our heads that most DOC is refractory "yellow stuff" which is metabolized by bacteria, but only very slowly, and probably doesn't constitute in terms of this low oxygen a great demand at all. But when we ran some of the calculations with these BOD experiments we have done and then back-calculated to carbohydrate available in that dissolved pool, they were showing up in the mg/l range -- about 1 mg/l -- which in my experience seems high and I am just interested in just how much that labile DOC pool drives the system.

Kemp: Just a comment -- I would be curious in seeing those data -- but just using the standard digestion analysis for DOC and then doing mixing diagrams, DOC behaves by and large conservatively. If you look at time series for a single station over the course of a year, it doesn't change much.

Jonas: Right! The point is that it is mostly refractory material, condensed, high nitrogen, humics -- if we are in fresh water -- probably from phytoplankton, aliphatic stuff condensed in the Bay, and it is not labile, not available, and it's very constant. Frankly, DOC is a silly thing to measure if you are interested in these driving forces, but the problem we run into in this bacterial side, it looks as if some of the dissolved material is driving the system in some cases, particularly in the deep water in the summertime, where the proportion of the total BOD -- the labile C estimate -- sometimes up to 90% will pass through that GF/F filter. Now what that is exactly is still a question in my mind, but it looks like there is a high level of what we are functionally calling "dissolved." And I am just interested in that proportionate driving force. Measuring DOC in an analytical sense is probably not a useful measure for any of these rate process-oriented things.

Ulanowicz: I have some other figures for you — if you take that 95,000 figure as being reasonable -- the output from the DOC to the free bacteria -- then that ramifies to ap-

proximately 7-12% of the indirect diets of your filter-feeding fish (nekton) which seem to have the highest sensitivities to that particular transfer. I can tell you that from how this network is now constructed. If you take issue with that particular flow, why that could change.

Question: Taking this up to a higher level, I would be curious about the data you present on sea nettles because it is my impression that we know quite little about their feeding rate and their excretion rate, yet at the end of your talk when you look at the recycling controls, they were the dominant organisms in terms of feedback in the pelagic part of the water column. How did you get that data? Was this by difference, or. . .?

Baird: Well, that was mainly Dave Cargo's data that he has collected over quite a number of years. And the values incorporated into this model are based on an average of the last three years' numbers. There is information available on their feeding, ingestion, and respiration rates and so forth. That is how that compartment evolved.

INFLUENCE OF LOW OXYGEN TENSIONS ON LARVAE AND POST SETTLEMENT STAGES OF THE OYSTER CRASSOSTREA VIRGINICA

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Our interests in the influence of low dissolved oxygen tensions on the early life stages of the American oyster Crassostrea virginica were stimulated by consideration of two scenarios. Oyster larvae occur in the tributary estuaries of Chesapeake Bay during a period of the year when low dissolved oxygen levels have also been recorded. The literature strongly suggests that larval retention in estuaries is influenced by active depth regulation of those larvae at or near the level of no net motion. If this is indeed the case, then larvae may be exposed to lowered oxygen tensions. The literature, including contributions by PIs of this project, also suggests that the lipid-protein based energy metabolism of bivalve larvae is incapable of supporting an anaerobic energy metabolism.

Two questions from this "larval scenario" arise: (1) is the swimming behavior influenced by low dissolved oxygen tensions, i.e., do larvae close and sink to the bottom where they may be eaten by benthic organisms, or do they actively avoid low dissolved oxygen and thereby compromise their optimal depth regulatory mechanism for retention? and, (2) can larvae maintain swimming activity under reduced dissolved oxygen tensions, i.e., do they continue to function aerobically at the same or reduced rate, or do they indeed have some anaerobic capability?

The second scenario involves the settling and early post settlement stages of the oyster. When larvae have matured to the point of being able to settle, they are called "competent." The settling (metamorphosing) stages (called pediveligers) have limited crawling ability for only a short time (hours), after which they cement themselves to the substrate and remain sedentary. Again, contributions by the PIs suggest that these stages gradually undergo a transition from lipid-protein to carbohydrate-protein based energy metabolism. The latter is appropriate for anaerobic metabolism. The time course of this transition is not adequately documented. The question arises: if early post settlement oysters are exposed to low dissolved oxygen, for how long can they survive given their (inferred) limited capability for anaerobic metabolism?

With this as background, we defined several objectives to examine these questions or scenarios:

1. To examine the influence of low oxygen on ontogenetic changes in swimming rate and behavior of larvae, beginning with recently spawned individuals.

2. To determine the influence of low oxygen on behavior and settlement success in competent pediveliger larvae.

3. To quantify the influence of low oxygen on the aerobic metabolism and survival of post settlement juveniles.

4. To document the acquisition of the post-settlement capability to function anaerobically.

5. To compare quantitatively the contributions of aerobic and anaerobic components of energy metabolism from early larval to post-settlement life stages.

Our progress in meeting these objectives is as follows.

1. At the University of Maryland's Horn Point Environmental Laboratories, we have begun to examine the rate of swimming of larvae of five different size ranges (44-88, 88-149, 149-177, 177-210, >210 μm maximum dimension) exposed to oxygen-saturated seawater (approximately 15 ppt salinity), 50% and 20% oxygen-saturated water. Observations were made at regular intervals for up to 24 h after introduction of the larvae into the controlled oxygen regime. Exposure to 20% of full oxygen saturation for 24 h does indeed reduce swimming activity, with the pediveliger perhaps the most sensitive stage.

In addition, a number of experiments were completed to investigate geotactic behavior of these five size classes of swimming larvae at HPEL. We had anticipated that larvae would close their valves in the presence of low oxygen levels, thus sinking to the bottom. However, recent data show that larvae (except the smallest or youngest - 44 μm) tended to swim upward in our darkened experimental chambers to a greater extent than did control larvae in fully oxygenated conditions. There was a tendency for this negative geotactic response (swimming up) to be slightly more pronounced in water of 20% oxygen saturation than at 50%. Thus, although their swimming rates did slow somewhat by 24 h, larvae did not stop swimming as expected upon first exposure to low oxygen, but appeared to respond in a fashion that would bring them up into presumably more oxygenated water. We plan further replicates of these experiments in 1987.

At the Virginia Institute of Marine Science we have examined changes in swimming activity of similar size ranges of larvae as they are exposed to stepwise decreases in percentage saturation of oxygen over short periods; for example, 100% to 60% to 40% to 20% to 9% over a 4-h period. The use of a flow-through chamber avoided exposure of the larvae to an air-water interface. These studies were carried out at 25 ppt salinity. In all instances we observed the larvae to swim actively at all oxygen tensions (even 9%!). We did

behavior is underway or planned using a motion analyzer recently acquired at HPEL.

2. The findings above emphasize the need to focus on the pediveliger stage. At VIMS in late 1986, two experiments were completed in which competent pediveligers were provided with suitable substrate in a matrix experiment of three oxygen saturation levels (100%, 20% or 5% at 25 ppt salinity) and three temporal scenarios (one, three and five days exposure at the original oxygen level followed by a change to 100% saturation). The objective was to examine both survival and settlement success under these regimes. Data are presently under examination, and we hope to report on them at the January 1988 meeting. Again, further replicates are planned for completion in 1987.

3. We have been somewhat perplexed by the results from experiments designed to examine the third objective. While we have successfully generated a curve relating weight to oxygen consumption rate (VO_2) in post-settlement oysters of 1-6 weeks age (post settlement), we have made four attempts to examine post-settlement survival at 100% and 20% oxygen levels with confounding results. In two instances oysters survived with apparently no differences at both levels, whereas in the other experiments almost total mortalities were quickly observed (2-3 days) at the lower oxygen level, with some additional mortality also being observed in the 100% controls. Materials and methods were identical in all experiments, clearly indicating the magnitude of natural variability in these studies.

4. The enzymes alanopine and strombine dehydrogenase have been resolved for pediveliger larvae (pooled lots of 10 individuals) by thin layer polyacrylamide gels. The finding of ADH and SDH suggests capability to function anaerobically, but we do not as yet have a quantitative measure of this ability (see 5).

5. We plan to combine (4) above with this objective in a study of total heat production (microcalorimetry) and

respiratory heat production in collaboration with Dr. John Widdows at the Institute of Marine Environmental Research, Plymouth, U.K., in the spring/summer of 1987. The combination of calorimetry and respirometry is the only definitive method of demonstrating functional anaerobiosis in these early life stages. On completion of the study, Widdows will travel to University of Maryland and VIMS to undertake complementary feeding rate studies and, with the PIs, use the resultant data to generate an energy budget for the early life stages of the oyster under saturated and reduced oxygen conditions. We can provide details of the proposed methods to interested parties.

In summary, our data are obviously not yet complete, but our initial ideas on the inability of larvae to tolerate low oxygen for at least short exposures (hours) may need to be modified. Some tolerance is evident, although whether or not the larvae continue to function aerobically during this period is an open question. Clearly, the pediveliger stage appears susceptible to low oxygen stress, and we will continue to focus on this settlement stage in studies planned for 1987.

EFFECTS OF LOW DISSOLVED OXYGEN IN THE CHESAPEAKE BAY ON DENSITY, DISTRIBUTION AND RECRUITMENT OF AN IMPORTANT BENTHIC FISH SPECIES

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Although extensive summer oxygen depletion is thought to be one of the most important factors decreasing the capacity of the Chesapeake Bay to support economically important fisheries resources (Taft et al., 1980; EPA, 1982; Officer et al., 1984), little is actually known about the impact of hypoxic conditions on population dynamics of Bay fishes. Because of their limited ability to exploit the water column habitat, benthic fishes should be among the most severely impacted by hypoxic bottom waters. During 1987 I am examining the abundance, distribution and recruitment of a benthic fish species, the naked goby (Gobiosoma bosci), in relation to dissolved oxygen levels in nearshore oysterbeds in the mainstem Bay. The naked goby is among the most important prey species in the diet of commercially important piscivores. It can comprise 50% of the total, and the majority of the fish component, of the diet of juvenile striped bass (Wass and Wright, 1969; Markle and Grant, 1970). Naked goby larvae are also among the most abundant fish larvae in the Bay, frequently ranking first or second in abundance in summer collections conducted in Chesapeake Bay tributaries and nearshore waters (Wakefield, et al., 1977; ANSP, 1981; Normandeau Associates, 1981; Gallagher and Currence, 1982; Shenker et al., 1983). The potential impact of these larvae on the zooplankton on which they prey, therefore, is considerable.

Field observations indicate that naked gobies migrate inshore as dissolved oxygen levels decline. Several conse-

quences could result from such movement: (1) because they are dependent on oyster shells, etc., for shelter, extensive movement may greatly increase predation rates on these fish; (2) where shallow, sheltered habitat is not continuous with deeper habitat, mortality could be extremely high as fish are forced to either remain in low oxygen areas or enter habitat without suitable shelter; (3) considerable reproduction could be lost as nests containing eggs in affected areas are either abandoned or suffer high rates of egg mortality due to inadequate oxygen concentrations; (4) nesting activities in shallow areas may be disrupted as larger species (e.g., the toadfish, Opsanus tau) or more dominant goby individuals invade inshore sites; (5) because oxygen levels fluctuate as the pycnocline tilts, the combination of low adult populations and suitable shelter in deeper areas may result in high larval settlement during periods of adequate oxygen levels followed by high post-settlement mortality as oxygen levels drop. All of these effects of hypoxia could influence production and biomass of the naked goby in the Bay, and thus impact both the goby's predators and prey.

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BAY ANCHOVY ECOLOGY IN MID-CHESAPEAKE BAY

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The bay anchovy (Anchoa mitchilli) is the most numerous and ubiquitous fish in the Chesapeake Bay. It is a major consumer of plankton and is an important food of predator fish. Its population ecology in mid-Chesapeake Bay, including abundance, age, growth, mortality, foods, fecundity, spawning and recruitment patterns, is being studied with Maryland Sea Grant support. Anchovy and zooplankton distributions relative to a tidal front near the mouth of the Patuxent River were the focus of sampling in 1986. Trawl sampling will continue in 1987 but, in addition, laboratory experiments on oxygen tolerances of anchovy adults, eggs and larvae will be determined. Future research objectives will include ration estimation and production estimates in the laboratory under hypoxic and adequate oxygen conditions. Results will be important to predict how low oxygen conditions can affect anchovy production/biomass and how impact of this abundant planktivore on zooplankton food can be altered by a hypoxic environment in Chesapeake Bay.

A transect beginning in the mouth of the Patuxent River and extending offshore 4 km into the Bay was sampled from June to November 1986 with a 16-foot trawl. Catch per unit effort (CPUE) varied greatly but mean CPUE increased from 200 to 1,025 individuals per 10-min trawl tow between July and September, the increase reflecting recruitment of young-of-the year anchovy that first occurred in August. Preliminary aging, based on annuli in otoliths, indicates at least three year-classes (0+, I+ and II+) in the population. Length-frequency distributions are multimodal, indicating the presence of two or more year-

classes. Spawning by anchovies is serial and not all females ovulate each day. Hydration of oocytes, ovulation and spawning appear to occur only at night. A transient, tidal front just offshore of the Patuxent River mouth, which develops on ebb tides and disperses on the flood, frequently had large concentrations of surface-schooling anchovies near it. The frontal region was mapped, its hydrography charted, and both anchovies and zooplankton were sampled near it to determine if the convergent feature concentrates organisms suitable as anchovy prey. The 1986 samples and data are being analyzed at present.

The 1987 research will include O_2 tolerance experiments. An adult anchovy population has been established in the laboratory. We will attempt to induce spawning by the captive population to produce eggs and larvae for the tolerance experiments. Life stage-specific O_2 tolerance limits will be estimated. In the field we will sample eggs, larvae and adults in parts of the Bay where anoxia prevails to determine their distribution, abundance and condition relative to those from our standard sampling area, where anoxia is not believed to occur commonly.

Ultimately, we wish to know if low O_2 levels in Chesapeake Bay can or have impacted anchovy consumption and production. Extension of our scheduled laboratory research to include feeding rates, growth determinations, and metabolic rates under variable temperature and O_2 conditions will allow us (1) to estimate the impact of anchovies on the plankton community; (2) to determine the potential effects of low O_2 levels on anchovy physiology and population biology; and (3) to model the probable effect of low O_2 on plankton-anchovy-predator fish food webs.

DISCUSSION

Question: Roger, on the microcalorimetry system, since a lot of the energy budgets that I have seen based on phyto- plankton have involved estimates of the number of cells, is this system adaptable to putting in a known number of cells and getting, for example, the caloric value of a specific diatom?

Mann: You don't combust them in this system to get their heat -- their caloric content -- what you are doing is putting the living larvae, in our case, in sea water and then measur- ing the heat increase in the sea water due to the metabolic heat output of the larvae.

Question: How do you maintain low oxygen?

Mann: These are sealed containers, and initially we nitro- gen-flow the water down to as low DO as we can, and then aerate to get it up to the level we want. We add the food, and we have essentially a siphoning system where we put larvae, usually in one or two mls of water in the bottom of our container, and then fill by siphon until it overflows. As it is overflowing we put parafilm over the top, then a screw- top on that, so we end up with a sealed container with the larvae and the food, which is then maintained in the dark. The only thing that is really going to make a mess of your maintenance of oxygen tension are leaks in the system, which you take care of by having a dualed-sealed system, or respiration by the animals in it. If you look at larval respir- ation rates in the literature, we are working here with about 400 larvae in a container that is about 170 mls, and even if you leave them for the full 8-day period, the impact of everybody respiring at maximum rate would be a couple of percent.

Question: What about bacteria, wall effects, and that kind of thing -- do you filter the sea water to reduce those ini- tially?

Mann: The water has been one micron-filtered to start with.

Comment: That would probably not take out the bacteria.

Mann: It is not going to take out all the bacteria, no.

Question: But over 8 days, you don't see a significant decrease in oxygen tension?

Mann: We have never maintained them 8 days; everything gets a water change every 2 days.

Question: If you ever study actual anoxia for short periods, is there likely to be a difference between nitrogen-produced anoxia and naturally occurring anoxia that has H_2S in the water? What does that mean for these kind of experiments?

Newell: That is a good point — that is something that we need to work closely with you and others who are really looking at this. Because when we started our experiments, we didn't know exactly what the distribution of anoxic (totally anoxic with H_2S) water was, opposed to just hypoxic water. Once that information is more fully documented we can in the future actually look at effects of environmentally realistic levels of sulfide on the metabolism. Potentially, sulfide can be very important in poisoning the invertebrates.

Jonas: To give an idea of a seasonal cycle, when the water appears to be truly anoxic based on Winkler titrations early on in the season, the water column does not necessarily contain detectable sulfide. According to Jon Tuttle's work, essentially all this sulfide is coming from the sediments, not water column processes. As time goes on and these anoxic conditions persist, then the sulfide coming from the sediments does saturate, it moves up in the water column — you saw the gradients yesterday. Very rarely has he seen co-existing sulfide and oxygen. It happens, but it's very transient, and right near that pycnocline. It's probably a dynamic phenonemon. But in the advective oscillations that we are talking about, you can get substantial concentrations of sulfide being pushed up into these areas.

Comment: But the other point is that if you are concerned with the sediment/water interface, that is where sulfide should appear the soonest, after anoxia.

Jonas: Absolutely. And there are other reduced sulfur intermediates that people just wave their arms about; they are there — who knows if they are of any consequence, though the sulfide itself could certainly be a poison directly.

Newell: Our initial experiments will really be looking at the pure anoxic side -- the dissolved oxygen — but we need to address the sulfide.

Jonas: One other thing, kinetically, is that sulfide, if it is pulsed into an aerobic environment, does not disappear immediately. This year, because we had anoxia and were trying to do these BODs, we wanted to get rid of the sulfide because we wanted to know the organic component, not the inorganic component, of oxygen demand. And one could not get rid of it even by agitating it, by holding it for hours — six hours -- we still would have sulfide in the water. Jon Tuttle tells me that is a salinity-related phenomenon. Well, it does obviously oxidize chemically, but not instantaneously. The rates are reasonably slow, and might have an impact on organisms.

Mann: Are you getting any experimental or survey work, or any type of mapping of these levels of sulfide so that we can then use them?

Jonas: That was not part of the orginial objective, but we did institute sulfide analyses, so we have some data for the past year across that range of Bay from below the Potomac up to the Bay Bridge. One of Jon's students came out with us to do this.

Kemp: I think that there is enough data for you to establish a frame of reference for such experiments, but I think the point that Bob Jonas makes is that sulfide is really tough to regulate because unlike a lot of other metabolites you have a spontaneous oxidation, so regulating constant concentrations is a good trick experimentally.

Sampou: But you know it is going to be a problem, because there has to be some residual for hours. If Tuttle's data continue to be correct for subsequent years about seeing those high levels, higher than we have seen anywhere else this past summer -- very, very high levels of sulfide -- and if they are going to persist for six or eight hours, even low levels, they are going to be very toxic metabolically.

Comment: My understanding, at least of the chemical half-life of hydrogen sulfide, is on the order of 1-2 hours for half-life. So if you are starting with 100 micromolar mixed in, it might stick around a bit; if you start with 3 or 10 micromolar, that is pretty low, considering when your sediments are having up around 1100 micromolar.

Jordan: You can maintain reasonably stable sulfide solutions in the laboratory over a few hours, particularly if you have water that is low in oxygen to start with.

Newell: Jon was saying that you get quite good electrodes for sulfide -- have you used them?

Jordan: My experience is that they were totally useless in the natural systems -- you might be able to use them in the laboratory. The problem is that in nature, those electrodes only measure the free sulfide ion, so unless you are at pH 13, the free sulfide ion is present in extraordinarily low concentrations -- even if the probe nominally will get down to those numbers, there is so much noise that it is almost impossible to read.

Jonas: Actually, the detection scheme that they have developed -- that Chuck Divan has been working on -- is a spectrophotometric technique and is tested in various solutions. It is fairly straightforward, and they actually can preserve the sulfide, and so the analysis does not have to happen immediately.

Jordan: You can do those on shipboard, I know.

Newell: So it is easy in an experimental situation to monitor sulfide levels?
Jonas: Sure -- it would not be a problem.

Purcell: I was wondering if we find the larvae of the anchovy and the oyster in the hypoxic waters -- I haven't seen any in situ information on that. I also don't really know how discrete these boundaries are -- if it is an abrupt jump into hypoxic waters or if it is a gradual transition. But I was wondering if the experiments with oyster larvae, for example, looked at gradients or at how the larvae behave at discontinuities.

Mann: We haven't tried DO discontinuities, but we tried salinity discontinuities, and we can make those work quite nicely. We can set up salinity discontinuities which the animals will swim through — totally ineffective -- and others where they treat them rather like brick walls. With that basis as a control, I see no reason physically why we can't build a DO discontinuity superimposed over a salinity discontinuity. So in terms of how do they behave at DO discontinuities, we don't know, but practically, I think we can address that question.

Jonas: When you were treating larvae with different DOs, did you see anything there?

Mann: No, the experimental set-up is as follows: A long, tall chamber sits in front of the video machine. When you irrigate it to change DO, you totally change the volume in the chamber over about five minutes. This gives you a vertical velocity through the chamber in the order of 0.1 mm/sec, which is lower than the swimming speed of the animal. If you sit and watch the video machine, you see a general upward movement of your whole population. As soon as you stop the peristaltic pump and essentially lock in the oxygen throughout your whole chamber, and we have done dye studies to make sure that we get adequate exchange, these animals will cascade down through the chamber and within 10 or 15 seconds they are swimming again. So in terms of whether they move through a discontinuity, I don't see that that is going to affect them markedly over a period of time.

Purcell: What about the in situ question -- do you find them in situ in the low oxygen waters?

Mann: One of the real problems I have in addressing this question is that oyster biologists have not traditionally gone out and worked in the field and looked at oyster larvae, because it is an extremely difficult thing to do easily. And on those occasions where individuals have tried to do this, it has usually involved hordes of graduate students simply because of the problem of looking at all the samples. We have tried to look at some of the molluscan samples that were collected in field studies.

Roman: We have been counting oyster larvae.

Question: Did you count oyster larvae or bivalve larvae?

Roman: Bivalve larvae.

Kennedy: See, once you have gotten them you have to identify them, and it is only until they get to be about 200 um or more that you can tell them apart.

Mann: Basically, what we are trying to do at the moment is to use specific gravity gradients to separate out the detritus from the bivalve larvae to give us a first cut. To give you an idea of the manpower involved, in late 1985 with Bob Byrne we did a study of a frontal system in the James River where we looked at a transect with six stations on it. We did this transect over 3 tidal cycles, so we ended up with 30-40 bottles of plankton. To sort those out and enumerate all the oyster larvae took something like nine man-months of energy. And so trying to go out and take plankton samples and hoping to find larvae in the first instance, and then trying to sort them out to be sure you are actually looking at oyster larvae versus other things is just an horrendous proposition, and I don't think it is even practical to try to answer that definitely in the field until you have the plankton sorting problem under control.

Newell: Jenny Purcell has a good point, because we needn't necessarily be concerned about what hypoxia does to oyster larvae — we could look at any bivalve larvae and see whether they are living — they should be affected in the same way. But I don't know if anyone is getting any plankton samples there — well, you are, Michael.

Roman: The few times we went out in August, we collected >64 micron plankton, which should include bivalve larvae, from below the pycnocline in the anoxic layer so we could get a rough cut as to whether bivalve larvae were there or not.

Mann: Still, there is a whole question about whether the distribution of really low O_2 water is anywhere near where the presence of oyster larvae matters — if there are no bars in the deep trough zone, then do we care if there are oyster larvae there?

Newell: Well, these larvae are in the water column for three weeks, and are carried essentially passively with the water flow — so they can move great distances, and can be carried through many types of water. If that water happens to be either hypoxic or anoxic, even if there isn't an oyster bar within 5 miles of there, they can still be affected. They never come out the other end — it is like a black hole, they just fall into it and never come out.

Purcell: I was going to ask Ed Houde, what about the anchovy eggs and larvae?

Houde: We should do some sampling probably along that Chop-Pax transect during the summer to look at this in relation to our oxygen tolerance work. Penny Dalton is going to defend a Master's thesis tomorrow where she looked at the egg and larval distribution of the Bay Anchovy based on Calvert Cliffs Power Plant collections, and her basic conclusion was that at the transect off Calvert Cliffs, which extended out into the deep trough, the eggs were most abundant offshore and in the bottom tows, which were done with a sled, one meter off the bottom. The anchovy eggs were at 22-25C, which you might expect to hatch in about

24 hours, so their duration in the water column is about one day. She didn't know whether they were dead or alive when they were caught, but the numbers of small larvae were also more abundant offshore, out near that deep trough, not associated with the bottom, but more or less equally distributed thoughout the water column. Fish eggs generally float; the anchovy eggs would float if the salinity were 25 ppt or higher, but I suspect what has happened is that they have been spawned in the midwater, near the surface, and have sunk down into that 20-21 ppt water near the bottom. What the implications are, I don't know. She has oxygen data only for 1972, '74, '76 and '77. There is a significant negative correlation between egg abundance and oxygen levels -- a simple correlation. You can be misled by these things, but there is one.

Question: What is the size range of the prey items for an adult -- mature -- anchovy? What is the lower size limit of their food? Are they particulate feeders, or filter-feeders?

Houde: I don't know what the lower limit is, but they are basically feeding on copepods, copepod-sized organisms. Anchovies are basically particulate feeders, zooplankton feeders.

Question: What about the larval forms, the critical first feeding? Is there such a thing for these? At that stage, what do they eat?

Houde: Well, people talk about critical first feeding, but I don't like to use the term myself. They are eating copepod nauplii or probably large dinoflagellates, and data that Sellner and Roman showed us yesterday indicates that this is pretty common stuff.

MARYLAND STOCK ASSESSMENT STUDIES

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The Estuarine Fisheries Program of Maryland DNR is presently studying the stock characteristics of seven species of finfish and blue crab. Striped bass, American shad, alewife herring and blueback herring studies are supported either by federal Anadromous Fish Act funds or Wallop-Breaux funds. Blue crab, yellow perch, white perch and weakfish studies are funded under the cooperative state-federal Chesapeake Bay Stock Assessment Committee.

The short-term objectives of these studies are to develop or maintain indices of yearly reproduction, develop relative measures of the size of the adult stocks, determine the seasonal age and sex composition, and monitor growth rates of target species. In addition to detailed data on the target species, each project also records data on the presence and abundance of other species in the sampling gear. For the most part, these community data have not been examined. Target species data should eventually yield estimates of the proportions caught by man, natural mortality, relative abundance of breeders and annual recruitment of adults to the population.

The long-term goal is to fit the data into a rational scheme for managing the harvests of these stocks. Management plans, which require such data, are in preparation or have been prepared for shad, striped bass, herring, white perch, yellow perch and weakfish.

Although routine environmental data (e.g., depth and temperature) are taken, it is not an objective of these sampling programs to examine the habitat and population

interactions in detail. Obviously the program is concerned with the effects of potentially lethal habitat conditions on stock because "natural" mortality must be sorted out of estimates of total mortality so that levels of fishing mortality can be estimated for management planning.

Hypoxia can potentially affect growth, migration and distribution; it can also produce direct mortality. With the exception of striped bass, there has been little published work on the potential effects of hypoxia on our target species. The speculative hypothesis on the response of striped bass to hypoxia (Coutant 1985) suggests the potential for a significant complication in establishing a management plan for the Chesapeake Bay which would fit under the present coastal management framework. Management of other target species may also be complicated by hypoxia problems.

Exchange of data and ideas between habitat quality researchers and stock assessors is a necessity, and the Estuarine Fisheries Program is willing to make its data available.

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QUANTIFYING THE SEVERITY OF HYPOXIC EFFECTS

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We want to emphasize that quantitative assessments of hypoxia can be carried further than they have been. This requires more useful quantification of hypoxic effects and, through collaboration between scientists and decision-makers, explicit interpretation of these effects. We believe that one or more formal indices of hypoxic effects can help structure these improvements to better define and assess hypoxic effects.

Assessment of hypoxia entails three elements:

1. Knowledge of dissolved oxygen concentration (DO) fields, generally through measurement.

2. Knowledge of DO dynamics, to understand what could be done about hypoxia.

3. Knowledge of hypoxic effects and their social importance, to help decide if anything need be done.

In the Chesapeake, progress is being made in understanding the DO fields and their dynamics. However, there appears to be little quantitative understanding, Bay-wide, of socially consequential effects of hypoxia (e.g., how much hypoxia limits oyster or soft shell clam production). This lack of quantitative understanding is marked, even to the extent of disparate professional views as to which effects are most important. We argue that it is important and relatively easy to quantify the severity of at least some

socially consequential effects; we use mortality in oysters as an illustration. Before indexing other effects (e.g., avoidance behavior and its population consequences in striped bass and blue crabs, or growth reduction in oysters), additional research may well be necessary to determine the social significance of these effects or even how to quantify them.

Further, if we are to really "help decide if anything need be done" we must go beyond simply quantifying effects. We must help interpret them. We must help decision makers determine how much hypoxia is acceptable. Only when governments have defined unacceptable hypoxic effects quantitatively can they establish defensible goals with regard to hypoxia.

With the help of other investigators we have developed an index of hypoxic effects primarily for decisionmaking purposes. First we need a readily understandable scale for the index. We use the same scale used for other indices in a series designed to quantify several marine pollution effects (Figure 1).

The index scale has three ranges:

0-1   no concern

1-10   warning range (justifies consideration, if "enough area" is affected)

>10   alarm range (justifies action, if "enough area" is affected)

For illustrative purposes, assume the index value of 10 corresponds to 10% hypoxic-induced adult oyster mortality over a summer season. In practice the lower boundary of the alarm range would be negotiated by the parties concerned, and decided upon by the appropriate decision makers.

Note that the index does not address how much area must be affected to justify governmental consideration or

action. This undoubtedly varies greatly from region to region, and we doubt that it can be usefully defined by an algorithm.

Now we can quantify hypoxic-induced mortality and help interpret it for decisionmaking.

When DO falls below a threshold value, depending on temperature, an oxygen deficit begins to build up in the oyster. A low dissolved oxygen episode is defined to occur during the time period when the DO is consistently below this curve, i.e., when oysters are accumulating oxygen debt. We want to index the accumulation of this oxygen debt as the episode progresses. In order to calculate the index for an hypoxic episode we need three things:

1. Bottom DO and temperature measurements over the episode, measured frequently enough to allow meaning-ful estimates,

2. Authoritative judgment that some percentage of hypox-ic-induced oyster mortality is unacceptable. (Other endpoints might be chosen; it is important that they be estimable endpoints that are important for environmen-tal decisions. For instance, we could judge that some percent of larval oyster mortality is unacceptable. This might well be a more sensitive measure then adult mortality, as has been suggested by some experienced investigators.)

3. Finally, we need some quantitative linkage between the DO field and the resulting oyster mortality.

It is not a major problem to measure the DO field in Chesapeake Bay -- not trivial or cheap, but it is more straightforward than other information and decisions needed to assess hypoxic effects.

Let's assume we have an authoritative judgment about unacceptable effects, for example, that 10% oyster mortal-ity due to low DO is socially unacceptable. Now, in prin-ciple, we could link DO to oyster mortality in either of two

ways: either by field observations or from the measured DO concentration and reliable dose/response relationships estimated in the laboratory, i.e., by determining what dose of oxygen deficit causes 10% mortality. It would be very difficult and very costly to reliably link DO to field estimates of oyster mortality, at least over the entire Bay, so we chose to use laboratory estimates of 10% mortality as functions of DO, temperature and exposure duration. We emphasize that existing dose response data for the oyster are not reliable enough to index all relevant conditions in the Bay. But these data are relatively easy and inexpensive to get.

We have used laboratory dose response data from Bill Stickle, Louisana State University. We can use Stickle's LC10 estimates to determine what environmental conditions will cause an oxygen deficit to build up, and how long it will take to kill 10% of the oysters (Figure 2). The highest concentration of oxygen at a given temperature that causes O_2 deficit is termed the "incipient lethal" DO concentration. Incipient lethal concentrations are specified by the vertical asymptotes of the LC10 curves of Figure 2. These concentrations are plotted in Figure 3. (In practice, the curves of Figure 2 should be fitted statistically. A four-parameter hyperbola seems to provide the best fit to this unusually variable family of curves, based upon several data sets for fishes and invertebrates.) Once these things are known then we can calculate the index at each station sampled. Each index value is the sum of daily doses of oxygen deficit:

$$\text{Index} \; = \; \sum_{\text{episode}} \; (\text{daily dose of oxygen deficit})$$

$$= \; \sum_{\text{episode}} \; (\text{weight}) \, (\text{incipient lethal-environmental DO })$$

Once the weights are calculated, the daily oxygen deficit is calculated. It is a function of the difference between the incipient lethal DO and the measured DO concentrations. This difference must be weighted in proportion to how fast 10% mortality occurs at the measured temperature and DO.

Figures 4, 5, and 6 give three examples of low DO episodes and the associated index values. These examples use Tom Malone's data from his transect of the upper Bay, just below the Choptank River. Observations cover most of the hypoxic season. Bottom waters near the western shore (Station 1, about 9 m deep) and near mid-channel (Station 3, about 25 m deep) had index values several times greater than the "alarm" range. It is safe to say that these areas were hypoxic enough in 1986 to cause greater than 10% oyster mortalities where oysters were present. Where oysters were absent, low oxygen precluded oyster beds even if other conditions were adequate. Oxygen declines at the last, near mid-channel example (Station 4, about 7 m deep) never fell low enough to cause oxygen debt, so the index was zero.

Comparable index values throughout the Bay would indicate how much of the existing and potential oyster beds suffer "warning" and "alarm" levels of hypoxia. Perhaps even more significantly, since governments are already committed to remediating hypoxia in the Bay, the index can help quantify how much remediation is needed to regain acceptable water quality.

As we emphasized, more laboratory measurements of hypoxic-induced mortality in oysters are necessary for reliable index values. These are relatively inexpensive measurements to make. Given more reliable LC10 curves, index values could be calculated for all locations at which we know the seasonal DO calculations, thereby characterizing areas of the Bay that are not affected by hypoxia and those in "warning" and "alarm" ranges of the index.

Further, some other hypoxic effects can be quantified and indexed. One could, at minimal cost, quantify growth reduction and mortality of oyster spat and larvae; and, at greater cost and less accuracy, quantify avoidance by blue crabs and other resource species.

The index makes explicit both specific hypoxic effects and their social importance, factors that are typically assessed in vague and ad hoc ways. We suggest that use of

the index would facilitate decisions about remediating hypoxia in more consistent and defensible ways.

Some will find the index too complicated. It is possible to define a simplified version, but we are reluctant to simplify by relaxing the tight linkage possible between hypoxia and effects. If decisionmakers require a less complicated index, simpler approaches to interpreting Figures 4-6 are evident.
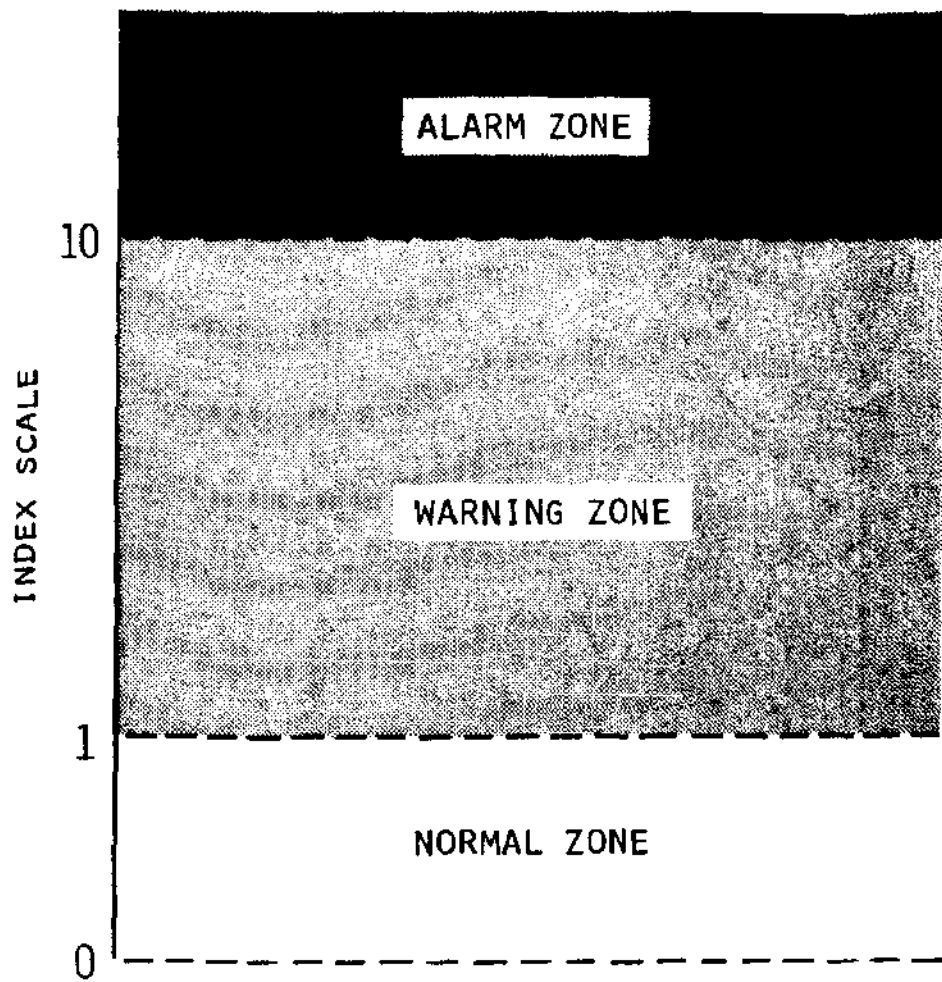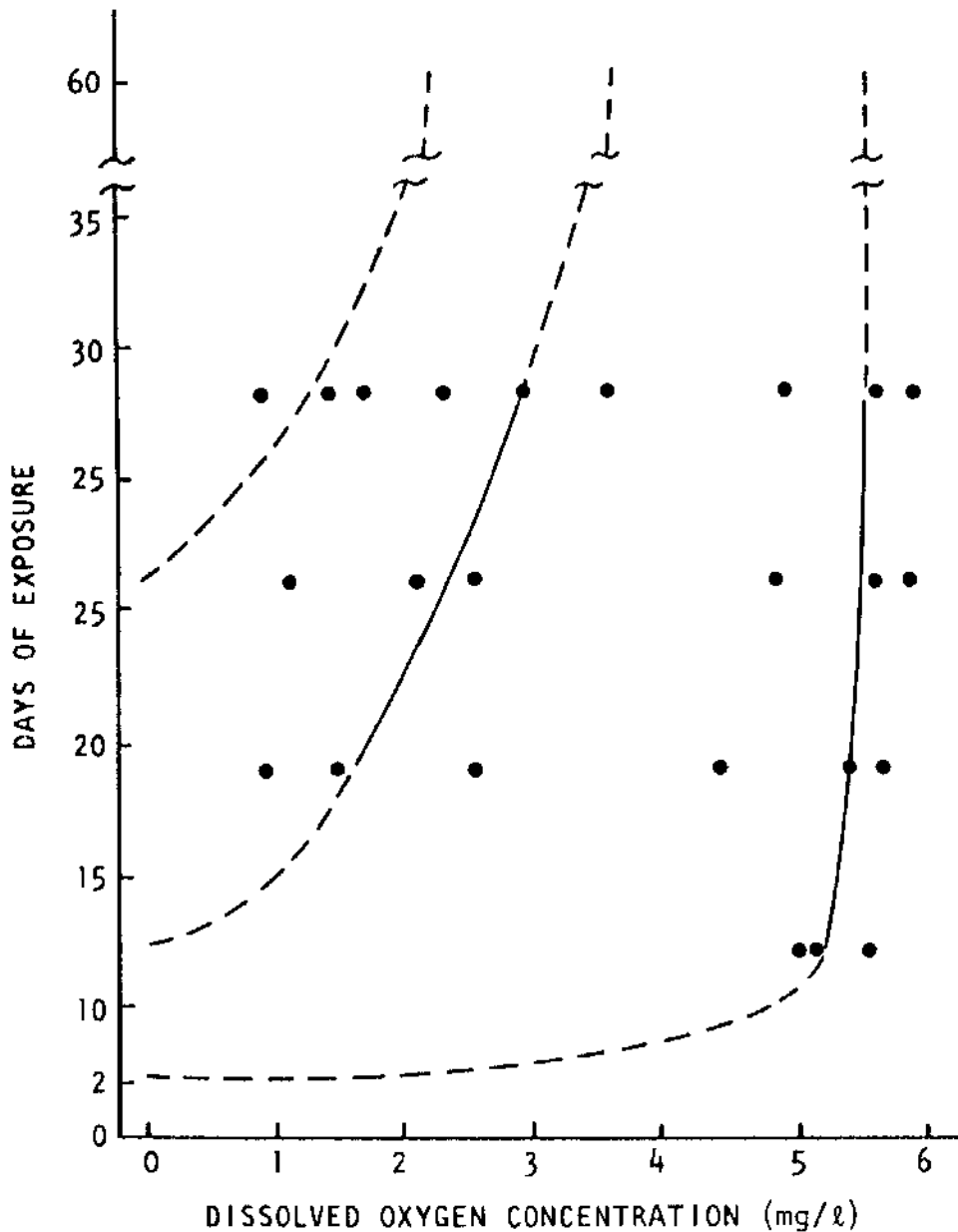
Figure 1. Scale and levels of concern for the index.

Figure 2. Days of exposure to reduced oxygen concentrations, at specified temperature, causing 10% mortality in the American oyster. The obviously uncertain extrapolations are for illustrative purposes only. Each circle represents an LC10 value based upon 20 oysters. (Data courtesy of William B. Stickle, Jr., Louisiana State University.)
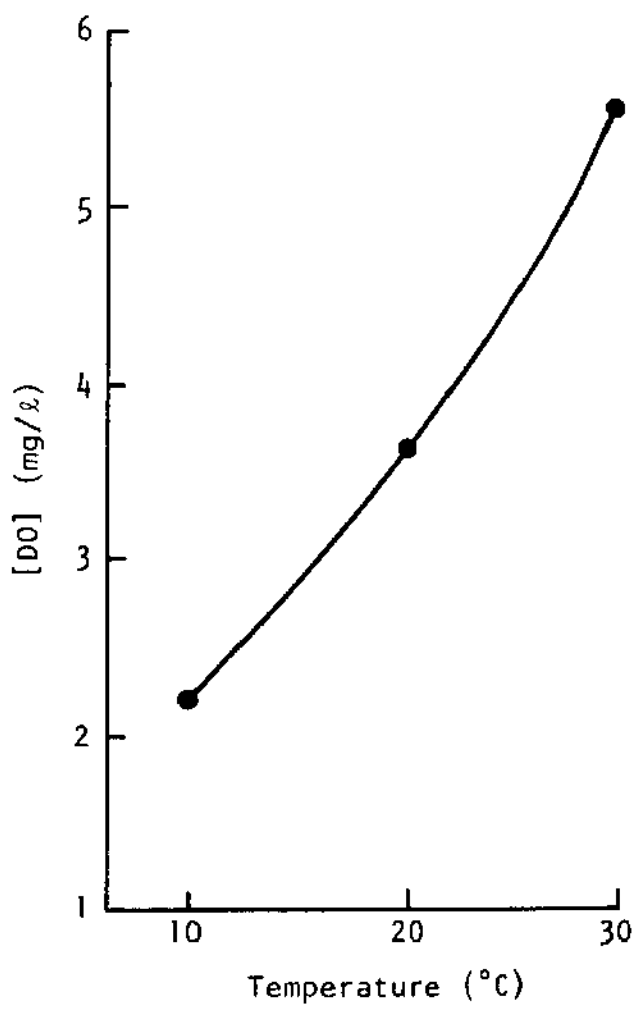
Figure 3. Incipient lethal (LC10) curve for the American oyster; the DO and temperature interactions just sufficient, over indefinitely long exposures, to kill 10% of adult oysters.
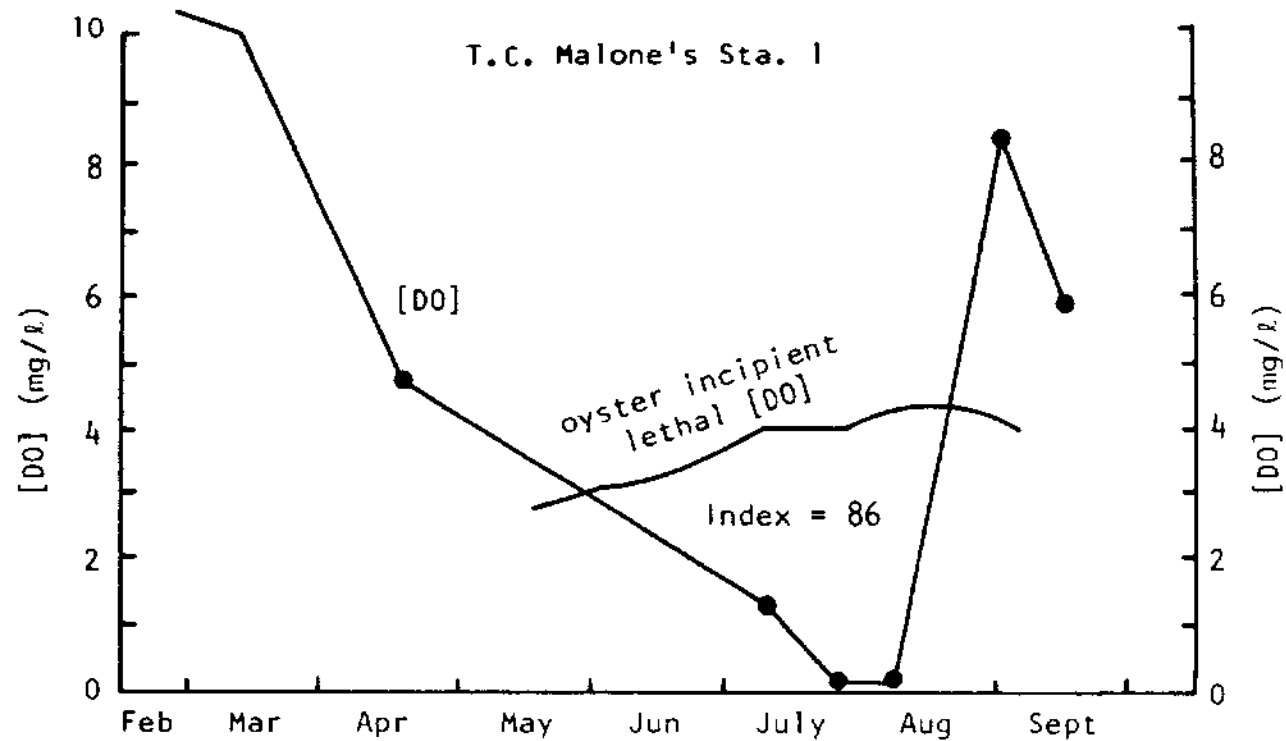
Figure 4. 1986 Seasonal (DO) and incipient lethal (DO) for oysters, in upper Chesapeake just below Choptank River (Data courtesy of T.C. Malone, University of Maryland.)
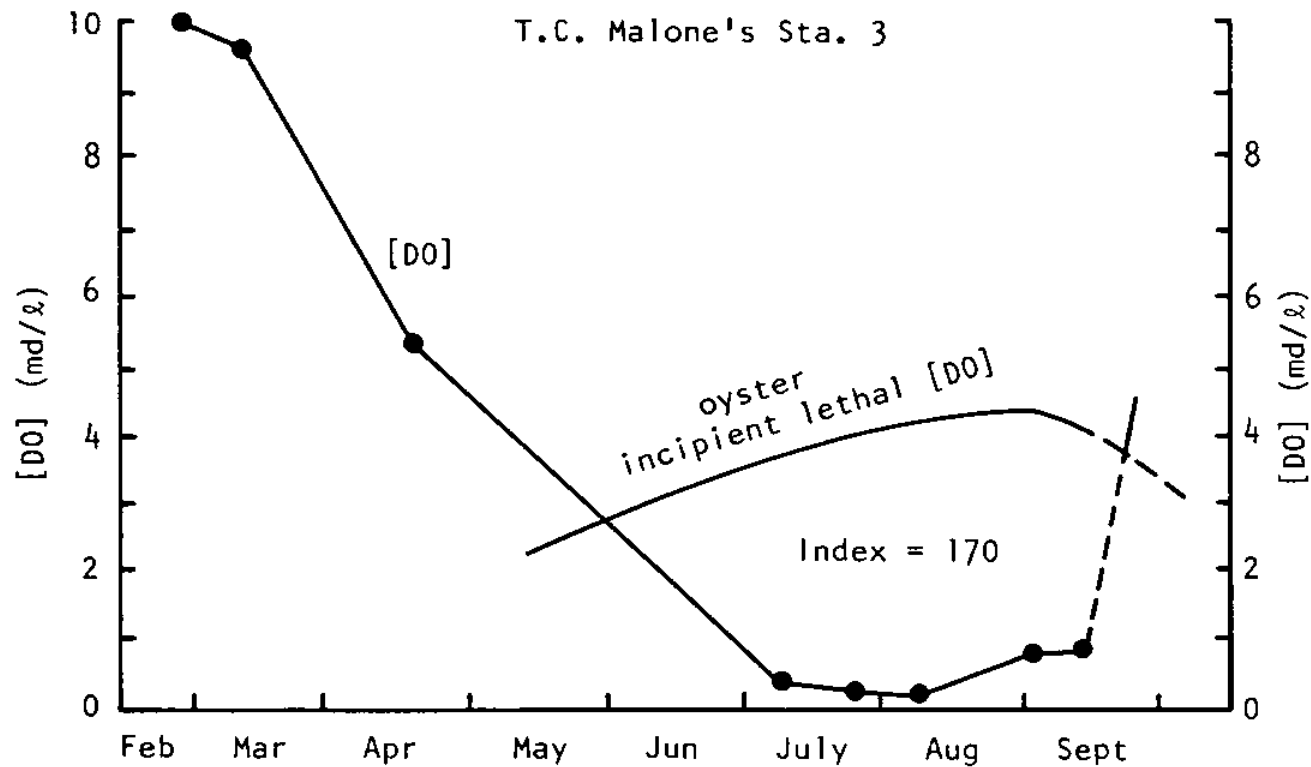
Figure 5. 1986 Seasonal (DO) and incipient lethal (DO) for oysters, in upper Chesapeake just below Choptank River (Data courtesy of T.C. Malone, University of Maryland).
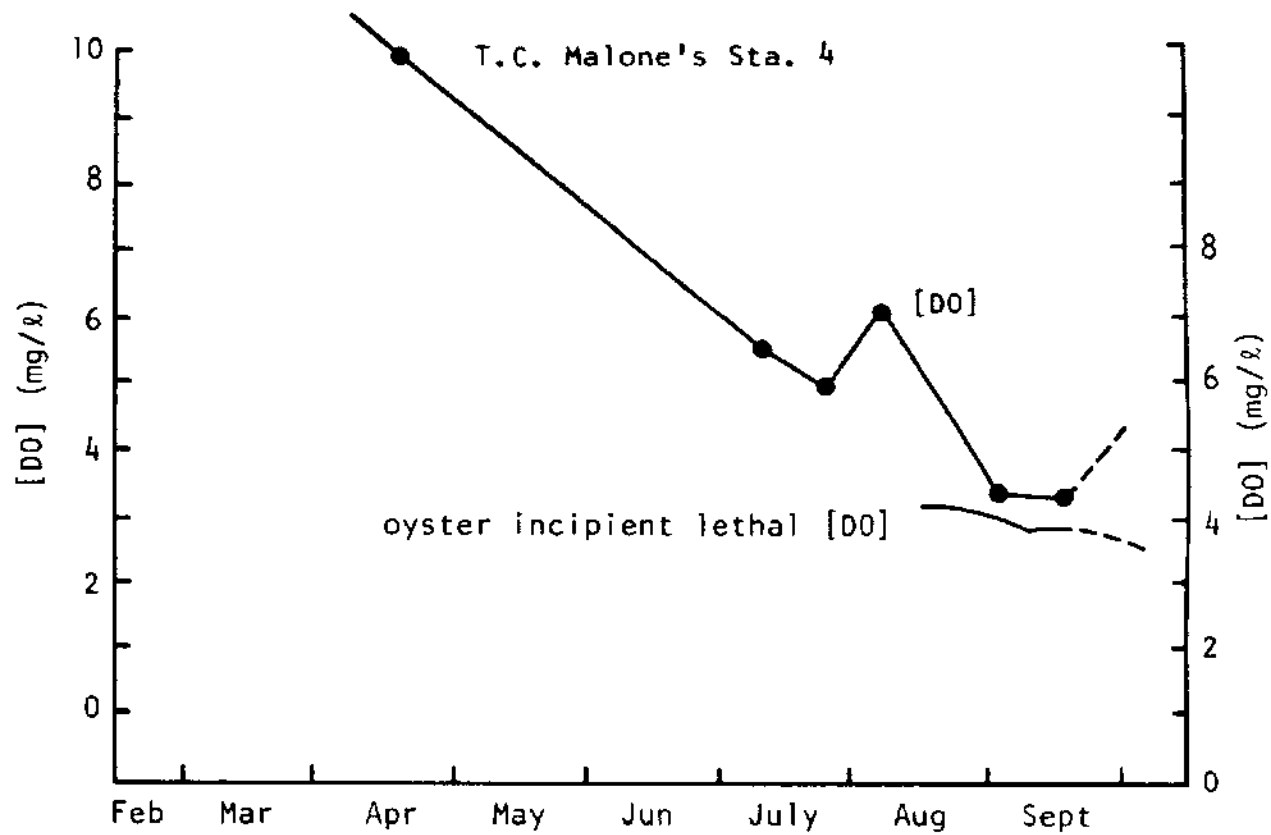
Figure 6. 1986 Seasonal (DO) and incipient lethal (DO) for oysters, in upper Chesapeake just below Choptank River (Data courtesy of T.C. Malone, University of Maryland).

DISCUSSION

Jordan: Were those LC10s measured on actively feeding oysters?

O'Connor: I am not certain.

Kennedy: This index, Joel, is it being used anywhere, as a management tool yet, or. . . what are the plans for the future?

O'Connor: It is not being used yet — I am shopping around for customers, looking for decisionmakers who feel they have hypoxia problems that this approach could help resolve. I would like to work with them in actually applying the index. I feel that there are several areas where it could be applied, using this sort of data. For example, the surf clam further north around New York. The surf clam data are even less accurate than the oyster data. But one can make reasonable estimates that probably wouldn't be too far off. You know those incipient lethal curves have to be within reasonably small margins. For management purposes though, I doubt that the oyster data, for instance, would be adequate. That is what needs to be done: define the quantitative linkage between the oxygen fields and the effects more convincingly.

Houde: Can you use the index to look at things such as production? You mentioned that it could be used to look at the proportion of blue crabs that disappeared from an area.

O'Connor: Yes, all you need to do is define some measurable effect for which you are willing to specify that some degree of that effect is unacceptable. However, the index presumes that you can measure the effect, say the proportion of blue crabs escaping hypoxic areas. It seems to me that such avoidance is one of the most difficult of all hypoxic effects to measure reliably over large areas. I am not certain, for instance, that blue crab avoidance can be mea-

sured practically, with useful precision, over hypoxic areas of the Chesapeake.

Jonas: Along those lines, you have something like the issue of shipping live blue crabs, for example, the ability to survive shipping.

Mackiernan: In 1984, a lot of watermen reported that the live crabs seemed weak, a lot didn't survive shipping or even getting to the dock. This was a bad anoxia year, so the crabs may have been very stressed.

Question: How sensitive is your index to the periodicity of dissolved oxygen measurements?

O'Connor: It assumes that the DO is continuously below that incipient lethal concentration -- that if you have something like diurnal or aperiodic infusion of oxygenated water, it just doesn't apply, because I just don't know how fast different organisms can repay that oxygen debt. With salmonids, they think it is on the order of 24 hours. And I don't know many other organisms for which this measurement has really been made.

Comment: So your index would be really most appropriate in the deep basins, but in areas where you have this tilting occurring, in the shallower areas, you have a problem on how often you go out and measure your dissolved oxygen event.

O'Connor: Right, what you could do in a case like that is measure the index over the longest period at which oxygen is continously below that incipient lethal concentration. And that would be the conservative estimate of the effect over the whole season.

Question: You only need one episode?

O'Connor: Right, but for something like oysters, for all I know it may only take something like 3 hours of oxygenated water and they can repay all of this oxygen debt.

Houde: From the point of view of both water quality and living resources, I think the idea that Robert Magnien had yesterday to put some deployed DO sensors out there would probably make a lot of sense. You could get an integrated effect of the time exposed to low oxygen.

Thomas: The Bay Program's exploring doing just that.

Boicourt: So are a number of investigators.

Sellner: Larry Sanford and now Denise Breitburg and myself have been talking with Endeco about simply getting a long-term continuous monitoring of DO. The Hydrolabs that we were going to use are essentially poisoned by sulfide -- not the probe, but the whole piece of equipment has to be sent back every time sulfide comes in. So at $500 a pop it is a little difficult to get measurements.

Breitburg: They will probably be useful in very shallow water where you are not likely to get the sulfides, and then you can use the Endeco ones in the deeper waters where you are going to get some sulfide.

Sellner: Actually, it is a great idea but seems rather difficult right now to do it, because there is apparently only one continuous DO-monitoring piece of equipment available.

Houde: Is there anything specific planned in the CBSAC group to look at hypoxic effects on fish, crabs or oysters?

Hennemuth: Not immediately, however we are going to pick the white perch and maybe one other species, and do some trial assessments with the methodology we have and are developing. And if we can square away how to do this kind of thing, we will probably move on to priority species that tend to come up. I am not so sure that since these analyses are mostly retrospective, they require some time series data base. I am not sure whether the historic data base is adequate to do this for any species. It may vary from one species to another -- we talk about doing this, but it would depend on where and when the low dissolved oxygen occurs relative to the species.

Houde: I guess you are right -- there are not many data to do anything with in a retrospective analysis.

Hennemuth: There hasn't been much -- in 10 or 12 years of data -- it is uneven.

Jonas: Two things relative to that -- one is, within these NOAA/Sea Grant DO projects for 1987, Dr. Peter DeFur from George Mason is going to work on the hypoxic influence on molting blue crabs. He believes they are under severe oxygen stress at this time. During the molting period, they are unable to ventilate, and any stress at that period might provide a very sensitive biological measure of the impact. They can't go anywhere, they are waiting and if one of these little oscillations appears to occur -- and even in the Patuxent, we have seen DO at the surface in the 3.0 mg/l range, up in the mouth of the Patuxent River -- then you might in fact have a severe impact on molting crabs right there. The other thing to note in passing, is that some of Dave Cargo's oxygen work from 1957 after the incident of mortality of blue crabs in crab pots, -- I think it is a CBL technical report, I don't think it is out in the open literature anywhere -- there is some data for blue crab survival, and that sort of thing, in relation to dissolved oxygen.

SEMINAR ON HYPOXIA AND RELATED PROCESSES IN CHESAPEAKE BAY

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